THE FOSSIL SNAKES OF FLORIDA

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I. Introduction

For many years Florida, among the eastern states, has been recognized as an important source of Cenozoic fossils, both invertebrate and vertebrate. The material collected in this state since the middle of the 19th century has contributed materially to our knowledge of past faunas of eastern United States. However, as in other areas, the earlier studies in Florida dealt almost entirely with larger vertebrates, and comparatively little was known of the smaller forms that inhabited this region. The vertebrate paleontologist of that period considered the smaller Tertiary and Pleistocene species somewhat rare as fossils, and concerned himself chiefly with the study of the larger extinct animals.

New techniques of exploration and excavation opened up a new field in paleontology—that of microvertebrate paleontology. The considerable effort spent on collecting and studying small fossils during the last few years has greatly extended our knowledge of the evolutionary history of certain groups of animals. Snakes, formerly thought to be rather uncommon as fossils, have been found quite plentiful. Detailed studies on the past herpetofauna of North America constitute a new phase in paleontology. They are contributing concrete information on the evolution of a group of which virtually nothing was known a few years ago.

The excavations conducted at Vero, Melbourne, and Seminole Field, Florida during the early part of the 20th century provided most of the fossil snakes known heretofore from the eastern United States. However, these collections are composed mainly of the larger species. The new material accumulated during this study includes many species of smaller snakes previously unknown as fossils, and adds a number of new localities for other fossil forms.

Various systematic studies on modern animals have indicated that peninsular Florida played an important role in the evolution and dispersion of many forms inhabiting the southeastern Coastal Plain. The shape, position, and geological history of the peninsula have undoubtedly influenced former patterns of gene flow and the dispersal of organisms. Its present fauna suggests it to have been both a haven for relict populations and a focal point of speciation. Thus further study of the rich fossil deposits in this region may contribute materially to our knowledge not only of the extinct forms, but of the derivation of our present Coastal Plain fauna.

II. Materials and Methods

This study is based on many hundreds of fragmentary and complete elements of fossil snakes, most of them in the collections of the University of Florida. The fossil snake material in other collections was also examined. At least 36 species have been found as fossils in the State, ranging in age from Lower Miocene to Upper Pleistocene. As might be expected, Pleistocene fossils are much more numerous than those from the preceding epochs.

Vertebrae and ribs are by far the most common elements, although various cranial and mandibular elements are also represented in the collections. For the most part this study is based on the vertebrae. So far no one has found ribs to be diagnostic on even a generic level.

In peninsular Florida terrestrial vertebrate fossils are practically always found disarticulated in a soft matrix. The techniques most useful in extracting small fossils from such matrices follow, essentially, those outlined by Hibbard (1949a).

Many fossils were obtained from the bottom of stream beds with diving apparatus. Some of these were found in water-filled caverns as much as 80 feet below the surface. Many fossil elements were also found on the surface of the ground in several isolated localities. Material from stream bottoms, as well as from isolated finds, is of limited value as a basis for stratigraphic conclusions. These fossils are used here merely as substantiating evidence for conclusions based on material of known derivation.

The Florida fossil snake material is identified largely by comparing it with skeletons of modern species. For this purpose it was necessary to assemble a large number of snake skeletons, representing a wide variety of species. Skeletons of over 300 species of snakes, most of them New World forms, were prepared, though in many cases only a representative portion of the vertebral column was cleaned. All of the North American genera are represented in this material, as well as representative genera from the rest of the Americas and from the Old World. For some genera all the known species were examined. Skeletons of different subspecies were studied to obtain some idea of geographic variation, and in many of the common species individuals of different sizes were examined for ontogenetic differences.

The following abbreviations have been used in referring to specimens in collections: *AMNH*, American Museum of Natural History; *CNHM*, Chicago Natural History Museum; *FGS*, Florida Geological Survey; *MCZ*, Museum of Comparative Zoology; *UF*, University of Florida Collections; *UMMP*, University of Michigan Museum of Paleontology.

III. FOSSIL SNAKE LOCALITIES OF FLORIDA

Among the eastern states, Florida is exceptionally rich in fossil remains of Tertiary and Quarternary land vertebrates. Fossil land vertebrates of this area are known from three epochs, all of which contain snake remains: the oldest are from the Lower Miocene, some occur in the Middle Pliocene, and finally, most abundant and widespread of all, are the remains from the Upper Pleistocene.

Chief among the features making Florida so rich in fossil material is that a soft, easily soluble limestone underlies a large part of the peninsula. Where these beds come close to the surface deep sinkholes and caverns are numerous. Such openings in the bed rock served as traps for land animals whenever the peninsula rose above the sea and sinkholes began to form. In addition, innumerable ponds and small lakes formed in the shallower sinks, each containing a rich fauna that became, in part, preserved in the bottom sediments.

There is another group of vertebrate-bearing deposits in the peninsula that have little, or no relation to the underlying limestone. These are the Pleistocene deposits formed close to the sea, either in old stream beds or in low coastal marshlands.

The classic localities of Florida represent both major types of deposits. As the fossil-bearing zones are relatively superficial, rivers and streams have cut through them and thoroughly mixed the faunas from different epochs in some localities. Earlier paleontological studies, based at least in part on such mixed deposits, have led to considerable confusion.

Not a few authors have mentioned the difficulty encountered in deciphering the past Florida faunas, especially in the central part of the peninsula. The reasons are found in the geologic history of the region and the nature of the sediments. None of the splendid sections which display faunal sequences so clearly in the West occur here. Solution of the underlying limestone has been highly active since at least Miocene time. The resulting sinkholes and caves have accumulated animal remains as small isolated deposits ever since. The deposits of any small geographic area may represent a considerable part of the Late Tertiary, so that a small sink containing Miocene vertebrates may be only a few feet from another sink containing Pliocene or Pleistocene remains. Thus, in Florida, vertebrate paleontology must, of necessity, be conducted on a detailed scale. Each sinkhole is a unit in itself, containing a fauna which may or may not be related to that in the next sinkhole. Unfortunately, this point has been emphasized too infrequently in the literature and has resulted in considerable confusion.

Because many of the localities from which fossil snakes have been collected have not been adequately described, or because they are new and have never been described, a short account of each deposit containing snake fossils is given. I hope that these remarks may somehow contribute to future correlation between the various localities in Florida. Most of the elevations in the following descriptions have been taken from Gunter, *et al.* (1948).

A. *Miocene Deposits*

The only Miocene locality from which snake remains have been taken is the Thomas Farm in Gilchrist County (R15E, T7S, Sec. 20). This deposit is usually considered Lower Miocene (Zone B), Arikareean (White, 1942a; Wood, *et al.*, 1941; Cooke, 1945; Romer, 1948; *et al.*). Several vertebrate groups from this deposit have been studied in some detail.[1] The most important paper that relates to the present study is that by White (1942a), in which the geology and paleoecology of the deposit are discussed in some detail. White postulates, on the basis of both faunal and stratigraphic evidence, the presence of an island in this part of Florida during the time of deposition. The marked similarity between the Garvin Gulley fauna of Texas and the Thomas Farm suggests that the isolation of Florida at this time, if it did occur, must have been short-lived. From the stratigraphic standpoint the evidence is not altogether conclusive. More detailed geologic studies are needed in the area between this and the Georgia-Florida boundary to determine the Lower Miocene geography of Florida accurately.

White believes the Thomas Farm deposit represents an old stream channel. This he bases mainly on the nature and disposition of smooth, rounded limestone boulders which, in a large part of the pit, seem to form a bar-like deposit. Similar rounded boulders are now known to form by solution in many of the sinkholes in Florida. Many of the boulders at the Thomas Farm are rather large. A stream of sufficient velocity to carry such loads requires a considerable gradient. Realizing this, White postulates fairly high elevations for this part of Florida during the period of deposition. Though really good evidence is lacking, most geologists refute such elevations during the Lower Miocene.

The presence of the genus *Siren* in the deposit (Goin and Auffenberg, 1955) suggests slow-moving or still water. Only one fish vertebra has been found in the deposit so far, whereas in known fossil stream deposits such elements are very common. On the other hand, they are frequently rare or absent in sinkhole, fissure, and cave deposits. More recent evidence (Bader, 1956) indicates that the fossil-bearing beds are much more steeply inclined than would be expected in a stream deposit. However, steeply dipping beds are to be expected in a sink, fissure, or cave deposit. The surrounding area is well marked with ancient sinkholes, and Cooke (1945) advocates sink deposition. Bader (1956) apparently favors this interpretation.

A point not previously sufficiently emphasized is the fact that remains of small rodents and bats are quite numerous, especially in the boulder bed. Accounting for the abundance of these small animals in a stream deposit is difficult, particularly in view of the fact that such remains occur commonly only in caves and fissures in a number of karst areas throughout the world. At present these animals commonly live in caves, fissures, and in the crumbling walls of steep sinkholes. Therefore from both a faunal and stratigraphic standpoint the writer interprets the locality as representing a linear fissure in the Ocala Limestone which became filled with clayey sediments during a relatively short period in the Lower Miocene.

The absence of any noticable depression at the surface of the present site has been used to argue against sink deposition, but there is no reason to suppose that the present land surface reflects such minor details as might have been present during the Miocene. Considerable exploratory drilling throughout the peninsula has shown many irregularities on the surface of the Ocala Limestone underlying the relatively flat Recent surface.

The writer presumes that if seas encroached on the peninsula they had a planing effect, smoothing much of the limestone bedrock by wave action. This is well illustrated along the upper edges of many limestone quarries where the projecting peaks of a typically developed karst topography have been evenly truncated. Marine erosion in the relatively low-lying Thomas Farm area easily could have removed much of the upper portion of what was perhaps at one time a deep and steeply walled sink or joint fissure. As the supposed Hawthorne Clay overlies the eastern part of the deposit, seas of Hawthorne time may well have truncated the projecting peaks. On the other hand, practically any of the high seas during Pleistocene time could have been responsible.

The Lower Miocene age of the deposit is based partially on correlation with vertebrates from western localities, partly on the nature of residual material and, to a lesser

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[1] *Mammals:* White, 1940, 1941, 1942a, 1947; Romer, 1948; Simpson, 1932; Wood, 1932, 1947; Lawrence, 1943; Bader, 1956. *Reptiles:* Vanzolini, 1952; White, 1942b; Williams, 1953. *Amphibians:* Tihen, 1951; Goin and Auffenberg, 1955; Auffenberg, 1956. *Birds:* Wetmore, 1943; Brodkorb, 1954a.

extent, on the overlap of a deposit believed to represent the Hawthorne formation of Middle and Upper Miocene. The vertebrate fauna of the Thomas Farm is not identical to the well known Arikareean. This might be expected on geographical grounds alone (Romer, 1948), or may be due to a slightly different time period being represented (Wilson, 1959). The residual materials point to post-Suwanee time. The eastern end of the deposit is overlain with a clay referred to the Hawthorne, though the clays of Florida, and especially those of the Late Tertiary, are difficult to define on general lithology alone. These clays are in turn truncated by a sandy clay, presumably Pleistocene in age.

The fossil snakes now known from this deposit include the following forms: *Pseudoepicrates stanolseni* new genus, *Ogmophis pauperrimus, Calamagras floridanus* new species, *Aniliioides minuatus* new genus and species, *Pseudocemophora antiqua* new genus and species, *Paraoxybelis floridanus* new genus and species.

The material from this locality provides our first glimpse of anything representing a rich snake fauna during the Miocene of North America. This period marks the first occurrence of the Colubridae in the New World, and also marks the last appearance of the large boids in both North America and Europe.

B. *Pliocene Deposits*

Fossil snake remains are known from two localities which seem to represent the Pliocene. These are:

Haile VI

Locality A.—(R 17 E, T 9 S, NW¼ and SW¼, Sec. 24): 0.2 miles east of Route 235, near the town of Haile, Alachua County; elevation approximately 84 feet. The stratigraphy of this deposit is as follows:

3. Recent sod and a thin black to gray sandy soil .... 3 in
2. A yellowish clay, weathering to red, containing lenses of a white to grayish clay; very smooth eroded Ocala Limestone boulders in the basal portion, with many small phosphatic grains which may or may not be cemented together to form rounded smooth boulders as much as 6″ in diameter .... 3-4 ft
1. Ocala Limestone (very irregular).

Fauna.—Bed 2 contains remains of the following snakes: *Heterodon brevis* new species; *Diadophis elinorae* new species; *Stilosoma vetustum* new species; Elapidae ? genus; Crotalidae ? genus.

Several members of the family Sirenidae have been reported by Goin and Auffenberg (1955), a glass lizard by Auffenberg (1955), and the anurans by Auffenberg (1957). The mammalian fossils have not yet been studied. Remains of fossil birds apparently are rare. The fossil fishes have been reported on by Caldwell (1956).

Correlation.—On the basis of the presence of *Hipparion, Serridentineus* and ? *Machairodus*, the deposit is here considered Pliocene. *Pseudemys caelata*, abundant at this locality, is known from only one other locality, Mixson's Bone Bed, which is considered by most workers as Pliocene. The snake fauna is different from those existing in either known Pleistocene or Miocene deposits from the peninsula.

On the basis of lithology, stratigraphy, and fauna, these beds seem to represent the Alachua formation, a non-marine series of beds sometimes considered contemporaneous (in part) with the Bone Valley Gravel formation. The present locality is in or very near that usually indicated as the Alachua Clay member of the Alachua formation (Dall, 1887, 1903; Sellards, 1910, 1914; Simpson, 1930a; Cooke, 1939, 1945; Cooke and Mossom, 1929; Parker and Cooke, 1944; Vernon, 1951, *et al.*). Cooke (1945) and Vernon (1951) correctly indicated that the Alachua formation represents at least portions of the Miocene, Pliocene and Pleistocene Epochs. However, Simpson (1930a) showed that the fossils in this formation are not always thoroughly mixed, as is sometimes contended, but are frequently found as discreet faunas in unmixed portions of many of the sinkholes. The present locality shows no indications of mixing, with the exception of a few worn shark teeth, apparently derived from the Hawthorne formation. Considerably more mixture is found in a Pliocene locality one-half mile west, where the upper bed of a fossiliferous deposit contains both Pliocene and Pleistocene faunal elements.

Both *Hipparion* and *Pseudemys caelata* currently are considered Middle Pliocene forms in Florida. However, the only well known terrestrial Pliocene fauna occurs at the Mixson locality (excluding the possible Pliocene forms in the marine-deposited Bone Valley Gravel formation). Other occurrences are scattered and the deposits contain no real *fauna*. The present locality may be an exception, but until the deposits are explored more fully and the mammals are examined in some detail it seems best to refer the locality to the Middle Pliocene; that is, perhaps equivalent to Mixson's Bone Bed (Simpson, 1929a).

Paleoecology.—The nature of the deposit and the fauna leaves little doubt that the locality represents an ancient stream deposit, perhaps close to the sea (Caldwell, 1956). The contained fauna shows no evidence of climatic conditions different from those now existing in the area. Knowlton (1927) and Berry (1916) suggest that climate in Florida during the Pliocene was similar to that at the present time. Extinct species of plants described from various Florida deposits are apparently ancestral to Recent forms (Berry, 1916).

Lithia Springs

Fossils have been found in the spring run, close to its head near the Alafia River, Hillsborough County (R 21E, T 30S, Sec. 16). The stratigraphic origin of the remains is unknown. The stream flows across the limestone facies of the Hawthorne formation, which forms the bedrock in this entire general area (Cooke and Mossom, 1929). The stream bed contains many phosphatic pebbles, apparently derived from the limestone, as well as fragments of Miocene marine vertebrates. The conditions of deposition are similar to those in the Peace River a few miles east.

Fauna.—Similar to that of the Peace River beds, in that Miocene, Pliocene, Pleistocene, and Recent elements are present.

Correlation.—The Peace River beds in the past have been considered Middle Pliocene in age (Dall, 1892). However, as Sellards (1915) pointed out, the streams in this area cut through Pliocene and Pleistocene mammal-bearing deposits. The fossils found on the bottoms of these streams are derived from older beds. Simpson (1929a) emphasized that fossils from such beds do not constitute a fauna. The fossils can be interpreted only by checking them against test faunas derived from localities where admixture has not occurred.

Only one snake vertebra was obtained from the bottom of the stream formed by Lithia Spring. Yet this element is different from those found in known Miocene or Pleistocene beds and represents a new genus (*Paleofarancia*), which is described below. It is much more heavily mineralized than most Pleistocene vertebrae. No Miocene land vertebrates are known from this part of the State. As this genus is not present in any of the Pleistocene deposits, and since many streams in this region frequently carry Pliocene fossils, the specimen is tentatively referred to that period.

C. *Pleistocene Deposits*[2]

For the Pleistocene deposits of Florida the difficulties in deciphering faunal succession are even greater than for the earlier epochs. The fossils are frequently isolated, are often mixed with older or with younger faunas, are seldom found in place and in many instances in the early explorations the exact location and horizon were unknown. To avoid confusion, data on fossil snakes are used only when the specimens were found in place, or of surely known derivation in a single locality with a considerable number of other species that are known to be contemporaneous.

In virtually all the papers describing various Pleistocene localities throughout the state, the standard section on which most correlations within the state rest is that at Vero, where three distinct horizons are manifest. The lowest, Stratum 1 of Sellards and

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[2] Pleistocene time as used here includes that period from the beginnings of the Nebraskan ice movement to the recession of the Mankato sheet (about 11,000 years ago, *fide* Libby, 1951). The suggestion by Flint (1942) to include all post-Pliocene time in the Pleistocene has not been followed. The term postglacial is too local and has no meaning in a nonglaciated area (Flint, 1942). For the same reason the "zero" varve of DeGeer (6839 BC) is too local. Distinct climatic changes in Europe (7912 BP), *fide* Zeuner (1950), seem to agree with the beginnings of the North American postglacial phase. There is little reason to believe that the extreme climatic changes experienced by more northern states occurred in Florida during the Pleistocene, although changes of lesser magnitude may be indicated by the fauna of several localities. However, these faunas have not yet been correlated positively with marine terraces or even with definite glacial or interglacial periods.

subsequent authors, is the Anastasia formation, a marine deposit. Above this is Stratum 2, a complex deposit clearly of Pleistocene age and containing a large land fauna. This horizon has been termed the Melbourne Bone bed (Cooke and Mosson, 1929), and is probably of Wisconsin or Post-Wisconsin age.[3] Above this bed is a stratum, more recent in age, which apparently represents at least some admixture of Pleistocene and Recent faunal elements and is known as Stratum 3. In this paper it is considered Recent in age.

To facilitate correlation of the Florida Pleistocene localities Simpson (1929a) set up a number of test faunas which contain many species of presumably contemporaneous mammals. These include Sabertooth Cave (Lecanto or Allen Cave), Citrus County; Seminole Field, Pinellas County; Melbourne Golf Course Locality, Brevard County; and Vero Beach, St. Lucie County. Only the faunas from Stratum 2 of the last three localities are considered as test faunas.

A surprising feature of the Florida Pleistocene vertebrate deposits is the marked similarity of the mammalian faunas from one locality to the next. This is well shown in Simpson's test faunas, where he assumes contemporaneity on the basis of faunal similarity. A number of new fossil localities have been discovered since Simpson's paper was published, and the faunas from each agree surprisingly well with Simpson's test faunas. Thus, the test faunas have not yet served to separate the Pleistocene deposits on their faunas alone. A possible explanation may be that the Pleistocene fauna in Florida, unlike that in other parts of North America, was relatively static and only slightly affected by minor climatic shifts. Faunal differences between deposits representing different periods in the Pleistocene may be much more subtle than those presented in periglacial zones. The mere absence of a faunal element can be due so easily to chance preservation or varying ecological conditions that it cannot be considered seriously unless it occurs over and over again. This has not been the case so far. Correlation of these deposits may be based much better on a study of the degree of morphological differentiation perhaps in the rodents of the various localities.

All the Florida Pleistocene localities so far known contain a surprising number of species of vertebrates indistinguishable from those inhabiting the same region today. This has been a major point in assigning these deposits to the Late Pleistocene. In well-known periglacial zones the Early Pleistocene apparently is distinguished by the fact that many of the smaller animals and most of the larger ones are extinct forms (Simpson, 1929a). Furthermore there is no evidence to support any concept involving greatly fluctuating climates for Florida on the basis of the known Pleistocene localities. All the Florida Pleistocene localities known so far possess fair numbers of large land tortoises, as well as other more southerly ranging reptiles, suggesting a warm climate for the periods represented by these deposits. An equitable Pleistocene climate in Florida is expected as the peninsula lies at a considerable distance from the periglacial zones. Davis (1946) reported spruce pollen from a peat bed in Leon County, but provided no information on its abundance. Isolated pollen grains can be expected in deposits far from their origin (Cain, 1926), and if Odum's (1952) postulate of high winds in southeastern United States during the Pleistocene is correct, even more caution is needed in interpretating pollen analyses in this area.

Pleistocene deposits of South Carolina contain remains of moose, walrus, elk, and seals. Although the walrus has been shown to be a warm water form, peat beds in the Carolinas contain considerable spruce and fir pollen, as well as twigs and branches of these trees (Berry, 1907, 1909, 1925; Buell, 1939, 1945; Frey, 1951, *et al.*). If taiga or boreal communities were common in South Carolina during glacial periods one would reasonably expect some sort of climatic changes in Florida, which should be noticable in the vertebrate faunas of at least some

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[3] Hay (1923) correlated these deposits on the basis of simultaneous extinction of related species widely separated geographically, and assigns Stratum 2 to the earliest Pleistocene (Aftonian and Nebraskan stages). There is no evidence to indicate that the periods of extinction of certain vertebrate groups in Florida coincides with those for related species in the periglacial zones (Simpson, 1929a). While the reference of this deposit to a substage of the Wisconsin is far from fully substantiated, it seems at present a reasonable assignment (Weigel, 1958).

of the Florida deposits.[4] Only a few northern vertebrates have been recorded from the Florida Pleistocene. However, Simpson (1929b) pointed out that the range of most superspecific taxonomic units was probably less restricted in the Pleistocene than at present. He also suggested the possibility that the native Florida animal population could not escape to the south, and thus its very presence would hamper the entrance of more northern types.

Another interesting feature of the Pleistocene deposits of Florida is that no genus or species is definitely known to have evolved into a new form during the time represented by the known deposits. The modern Florida fauna is simply a reduced Pleistocene fauna.

None of these deposits is over 100 feet in elevation and all seem to be located below the Pleistocene marine terrace level termed the Wicomico (Cooke, 1939; MacNeill, 1950). This indicates that no vertebrate fossil in Florida so far represents the maximum stage of the earlier interglacial stages. The known fossil fauna as a whole seems to reflect one somewhat characteristic of a climate essentially similar to that of the present, or possibly even one which could have extended into more southern climes (Simpson, 1929a). The known deposits probably represent Middle and/or Late Pleistocene time. Stratum 2 at many coastal localities may represent a substage of the Wisconsin, or even Post-Wisconsin time. This is substantiated by geologic evidence, though not conclusively (Cooke, 1945, *et al.*). Various fissure and sinkhole deposits in central Florida may be Illinoian in age (Brodkorb, 1957), as the fossiliferous zones lie below the presumed Wicomico terrace sands and clays, which some consider Sagamon in age. There are, however, some problems encountered in this interpretation: *i.e.*, the Wicomico terrace sands, presumably marine in origin, contain surprisingly few, if any, marine fossils; the Wicomico terrace level has not definitely correlated with Sangamon Interglacial deposits, which raises the question, are all Pleistocene fossiliferous beds below these terrace sands necessarily contemporaneous?

The simple fact that workers are not in agreement as to the number of terraces, their elevation, or even their mode of development, indicates our nearly complete ignorance in these matters.

Regarding correlation of the deposits, surprisingly few facts are known which bear on the problem. Some of the more important of these are as follows. (1) Up to the present time, no vertebrate fossil beds have been found at an elevation greater than 100 feet. (2) Fossiliferous vertebrate beds have been found at least 18 feet below sea level. (3) Adjacent sinks, caves and fissures may represent different ages. (4) There is no conclusive evidence that cold conditions occurred in Florida during any part of the Pleistocene. On the other hand, conditions warmer than those at present are suggested by the presence of large reptiles, such as *Geochelone*, which have been found in almost all localities. (5) Minor differences in faunal composition between many of the deposits are suggested in all three terrestrial classes. These differences could have their bases in ecology. (6) The modern fauna is largely a reduced Pleistocene one with many of the genera and species of Pleistocene mammals and birds now extinct. (7) Most genera (of at least mammals) in the Florida Pleistocene are typically found in the Pleistocene of other areas. (8) Some genera or species now found only to the north of Florida are present in the Pleistocene deposits of the State. (9) A number of fossil forms are larger than the same forms living in the peninsula at the present time. (10) On the other hand, many Recent species are morphologically identical with their Pleistocene ancestors. (11) Certain immigrant South American groups are present in most of the localities. (12) Some of the extinct genera or species are most closely related to forms now living in southwestern United States. (13) There has been some replacement on a specific, or subspecific level from Pleistocene to Recent.

Some features of the Pleistocene of Florida are frequently taken as fact, but in reality are only tentative points of departure in the absence of conclusive data. (1) Pleistocene climate was not greatly different from the present. The climate during glacial

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[4] Knowlton (1927) pointed out that the glaciers did not affect the vegetation of the periglacial zones greatly. In addition Flint (1942) and Bryon (1928) suggested that the periglacial zones in North America were probably much narrower than those in Europe, where glacial climatic effects are seen far southward.

stages may have been wetter than at present, and probably not much cooler. The interglacial climates were probably warmer and drier than that at present. (2) The terraces in Florida were formed basically during changes in sea level, though (3) upwarping in the peninsula during the Pleistocene may have modified terrace formation. (4) The Pamlico Terrace was formed during a stage of the Wisconsin, and the Wicomico during a stage of the Sangamon Interglacial. (5) All of the glacial and interglacial periods will eventually, on some basis or another, be recognized in Florida. (6) The ecological variation throughout the peninsula was as great during any one stage of the Pleistocene as it is today. (7) Similar populations of the same species, or the same genus, have had similar modes of existence during and since the Pleistocene. (8) Changing ecology brought about at least minor changes in the biota that can be recognized on analysis of the fossil record. (9) Most of the Pleistocene is represented by the deposits already known from Florida, though (10) the known deposits probably represent a greater number of Late than Early Pleistocene localities on chance alone. (11) The peninsula acted as a refugium, and as a center of speciation with island formation during interglacial periods.

There are a number of important problems which must be solved before workers will realize the full potential from these interesting series of Quaternary beds. (1) What were the extremes of temperature witnessed in Florida during the Pleistocene? (2) What is the total time represented by all of the Pleistocene deposits; of each deposit? (3) What is the exact extent of fluctuations in sea level, and when did these fluctuations occur? (4) What is the exact paleoecology of all of the major deposits in the area? (5) What is the extent of faunal admixture in each case?

Until more work is conducted in Florida on a detailed scale no one can assign positive ages to the known Pleistocene deposits of the area. A tentative correlation recently was attempted (Auffenberg, 1958a), but needs considerable verification before it will be of any use. Better correlation with terrace levels (marine, pluvial, or otherwise) is sorely needed. Further work being undertaken at the present time by a number of interested workers in Florida should shed considerable light on the interesting remaining problems concerned with correlation of these highly fossiliferous beds.

Fossil snake remains are now known from a number of Pleistocene localities throughout the peninsula. A description of each of these localities follows.

Arredondo, Pit I

A limestone quarry 4.2 miles west-southwest of Gainesville, Alachua County, just north of U. S. Highway 24 (R 19 E, T 10 S, sec. 22); elevation about 85 feet. Terrestrial vertebrate remains have been found on the northern and western sides of this quarry in clay-filled sinkholes, solution channels and fissures.

Locality A.—This is a vertical fissure 2 to 3 feet wide, extending from the surface of the Ocala limestone to an unknown depth below the bottom of the quarry. The fossils occur in a brownish to bluish clay, frequently with lenses of yellowish clay, weathering to reddish brown. For the stratigraphy and mammalian fauna of this locality see Bader (1957).

Fauna.—The snakes from this deposit include the following forms: *Carphophis amoenus, Heterodon platyrhinos, Drymarchon corais, Coluber constrictor, Masticophis flagellum, Opheodrys aestivus, Elaphe guttata, Elaphe obsoleta, Lampropeltis getulus, Tantilla coronata, Natrix sipedon, Thamnophis sirtalis, Storeria dekayi, Micrurus fulvius, Crotalus adamanteus.*

Correlation.—The mammalian fauna found in this locality suggests a Middle or Late Pleistocene period of deposition resembling closely that from Stratum 2 of various east and west coast localities in the state. Stratigraphic evidence at the present time suggests that the deposit may be Illinoian in age, but this is not definitely established.

Paleoecology.—The locality must have been located very close to a fresh water pond or stream on the basis of the fauna (*Tapirus, Neofiber, Siren, Pseudobranchus, Alligator,* etc.). On the other hand, such forms as *Geomys, Drymarchon,* etc. suggest open, dry forest conditions. *Pitymys,* which is known from the locality, usually inhabits dry forests or even scrub. The paleoecological conditions as interpreted on the basis of the known fauna differs little from that found in the area at the present.

Locality B.—A brownish sandy clay filling a diagonal fissure a few feet east of Locality A, and which may have been connected with it at one time, approximately 12 feet below the surface.

Fauna.—The only known snake is *Drymarchon corais*. Bader (1957) described the stratigraphy and mammalian fauna.

Correlation.—Middle or Late Pleistocene (Illinoian?).

Paleoecology.—Essentially the same as that of Locality A.

Locality D.—A brownish sandy deposit with large boulders of Ocala limestone, broken and eroded, filling a vertical fissure above Locality A, and possibly grading into it. Bedded sediments are evident in the lower 1-2 feet of the deposit. Above these beds is a reddish, homogenous sandy clay, which may be equivalent to Locality B. The fossils are well-mineralized, but sometimes somewhat chalky.

Fauna.—The following snakes are known from this locality: *Drymarchon corais* and *Elaphe guttata.*

Correlation.—Middle or Late Pleistocene (Illinoian?).

Paleoecology.—The entire fauna from this deposit suggests dry, open forested conditions, possibly similar to those existing in the same area today.

Locality H.—This deposit, located in the same quarry, but northwest of the area containing the deposits described above, is a horizontal fissure in the limestone. The fissure is approximately 3 feet thick, and about 18 feet from the surface. It is filled with a rather homogeneous buff-colored sand, containing small lumps of grayish clay.

Fauna.—The only fossil snake known from this locality is *Crotalus adamanteus.*

Correlation.—Middle or Late Pleistocene.

Paleoecology.—Too little is known of the fauna of this locality at the present time to warrant any serious ecological considerations.

Arredondo, Pit II

A limestone quarry 4.3 miles west-southwest of Gainesville, Alachua County, just south of U. S. Highway 24 (R 19 E, T 10 S, Sec. 22); elevation 85 feet. Terrestrial vertebrate remains have been found in place in a fissure on the west side of the quarry. For a list of the mammals collected there see Bader (1957). Remains of fossil snakes were collected from the spoil dumps, so that their exact origin is unknown, though they were undoubtedly associated with the extinct Pleistocene mammals.

Fauna.—The snakes known from this locality include the following forms: *Heterodon platyrhinos, Coluber constrictor, Opheodrys aestivus, Elaphe guttata, Cemophora coccinea, Stilosoma extenuatum, Thamnophis sirtalis.*

Correlation.—Middle or Late Pleistocene (Illinoian?).

Paleoecology.—The vertebrate fauna known from this locality suggests dry, open forested conditions very similar to those existing in the area at the present time.

Kanapaha I

A limestone quarry 4.8 miles west, southwest of Gainesville, Alachua County, just south of U. S. Highway 24 (R 19 E, T 10 S, SW¼ of SW¼ of Sec. 22); elevation about 85 feet. The vast bulk of the vertebrate fossils collected at this locality came from spoil dumps which originally filled a few solution channels and fissures in the Ocala Limestone on the southern side of the quarry. For this reason specific localities are not given.

Fauna.—The snakes known from this quarry include the following forms: *Drymarchon corais, Opheodrys aestivus, Pituophis melanoleucus, Elaphe obsoleta.*

Correlation.—Apparently Middle or Late Pleistocene.

Paleoecology.—The somewhat restricted fauna definitely points to a dry, open wooded area, similar to that in the area at the present time.

Haile, Pit I

A limestone quarry near Haile, Alachua County (R 17 E, T 9 S, SE¼ of SW¼ of Sec. 24); elevation about 84 feet. This is one of a series of limestone quarries located in the immediate area. The present pit is 0.4 miles east of State Highway 235.

Locality A.—This is a large opening in the Ocala Limestone on the west face of the quarry, and filled with bedded and steeply dipping laminae of clays, sands and fresh water marls. The stratigraphy of the deposit has been given by Brodkorb (1953).

Fauna.—The fossil snakes known from this deposit include the following: *Drymarchon corais, Masticophis flagellum,* *Elaphe guttata, Lampropeltis getulus, Natrix sipedon, Natrix cyclopion, Natrix* cf. *erythrogaster, Thamnophis sirtalis, Agkistrodon piscivorus.*

Brodkorb (1953, 1954b) listed the birds from this deposit. *Rana grylio* was reported from the locality by Tihen (1952).

Correlation.—Middle or Late Pleistocene (Pamlico?).

Paleoecology.—This locality evidently reprepresents an ancient fresh water spring head. This conclusion is based on both the stratigraphy and the vertebrate and invertebrate fossils. The beds are well sorted and the entire deposit is located in a funnel-shaped opening in the Ocala Limestone. In some parts of the deposit the sorted materials are definitely cross-bedded. On the other hand, the presence of dark laminated organic clays between lenses of sorted marls and sands seem to suggest still or slowly moving water. Faunal elements representing both stream and pond forms are common. Mixture of these units apparently has occurred so they do not reflect the alternating conditions indicated by the stratigraphy.

A reconstruction of the locality as it probably existed during the latter part of the Pleistocene would thus seem to call for an aquatic situation fluctuating between a flowing spring and a sinkhole pond. Sinks are common in the surrounding area, though water levels are so low that very few contain permanent ponds. Flowing springs are not found in the area at the present time.

Vernon (1951) discussed the possibility of the presence of a large Pleistocene river in this general area. It presumably flowed southward across central Gilchrist County, from the present Sante Fe to the Waccassasa rivers, and apparently occupied the Pleistocene valley of the Waccassasa River. He correlated this stream with Pamlico time, when sea level was thought to be approximately twenty-five feet higher than at present. The water table in large caverns in the immediate area varies depending on local rainfall, but is generally twenty-five to thirty feet below the surface. The river, perhaps larger than the Suwanee, was probably captured by underground drainage at the close of the Pleistocene.

The Pleistocene spring deposit at Haile I A probably represents the head of a stream that flowed westward into the larger Pamlico river described by Vernon. The rise of water table during this period allowed the spring to flow, whereas lowered water tables near the end of the Pleistocene caused the flow to cease altogether. Judging on the laminated nature of the deposit the spring probably flowed slowly for long periods of time, and may even have become ponded at different periods. Edwards (1949) reported an abandoned stream valley and spring head near the present Sante Fe River which may also date from this period. Aerial photographs of the area show no indications of any ancient stream bed.

Haile II

This is a limestone quarry 0.3 miles east of State Highway 235, near Haile, Alachua County (R 17 E, T 9 S, SW¼ of SW¼ Sec. 24); elevation about 84 feet.

Locality B.—The locality is represented by a horizontal fissure on the north face of the quarry, about twenty feet below the surface of the Ocala Limestone. The entire fissure varies from 1 to 4 feet thick, and extends back into the limestone for an unknown distance. Two beds make up the deposit. The uppermost is composed of a reddish sandy clay containing few fossils. Separating this from the lower bed is a thin band of limonitic clay, yellowish-brown to red in color, and which is found separating the same beds in many other sinkholes and fissures of the entire area. The lower bed contains considerable remains of rather small vertebrates, and is composed of a dark brownish, somewhat consolidated sand.

Fauna.—The snakes known from this locality include the following: *Carphophis amoenus, Opheodrys aestivus, Elaphe guttata.*

Correlation.—Presumably Middle or Late Pleistocene on the basis of the mammalian fauna (equivalent to Reddick I B?).

Paleoecology.—This deposit, because of the fairly large number of bat remains, probably represents a Pleistocene cave or fissure. The opening to the surface was presumably small, since larger bones are uncommon. The presence of *Ophisaurus compressus* (Auffenberg, 1955a, 1956b) suggests that an area of scrub vegetation existed nearby. However, the large bulk of the fauna indicates a more mesic, forested condition.

Haile IV

Locality B.—This deposit is located on the north side of a limestone quarry near

Haile, Alachua County, 0.1 miles west of State Highway 235 (R 17 E, T 9 S, SE¼ of NE¼ of Sec. 23); elevation about 84 feet.

The locality is a horizontal fissure in the Ocala Limestone, about one foot thick, but extending for a considerable distance around the quarry. It is located about thirty feet below the surface of the limestone. The only fossils found in the fissure so far are some limb elements of *Bufo* sp. and one vertebra of *Drymarchon corais*, all from just above the limonitic clay layer described under Haile II B.

Haile VII

A large limestone quarry near Haile, Alachua County, about 0.8 miles east of State Highway 235 (R 18 E, T 9 S, NE¼ of SE¼ of Sec. 24); elevation about 84 feet.

Locality A.—This locality is located on the northern end of the quarry. It is a large sinkhole depression from which the superficial layers have been removed during mining operations. The stratigraphy is as follows:

4. Reddish-brown sandy clay (?Wicomico Terrace sands)	3-4 ft
3. A stratum composed of many intergrading lenses of white sands, brownish to yellow sandy clays with numerous bits of eroded Ocala Limestone, etc.	3-4 ft
2. Bluish to bluish-gray clay, definitely bedded and found only in the lower parts of the deposit	3-11 ft
1. Ocala Limestone.	

Fauna.—The locality has an extensive mammalian fauna which has not been completely studied. The fossil snakes known from the locality include the following species, all from Bed 3: *Drymarchon corais, Coluber constrictor, Elaphe obsoleta, Masticophis flagellum, Heterodon platyrhinos, Heterodon simus, Lampropeltis getulus, Natrix sipedon, Thamnophis* cf. *sirtalis, Micrurus fulvius, Sistrurus miliarius, Crotalus adamanteus.*

Correlation.—Presumably equivalent to Arredondo I and Reddick I.

Paleoecology.—The nature of the beds and the associated fauna seem to indicate that this was a sinkhole pond. Bed 3 may represent the fluctuating borders of this pond.

Wall Company Pit I

This is a limestone quarry approximately 7.2 miles west of Gainesville, Alachua County, and 0.6 miles north of U. S. Highway 26 (R 18 E, T 9 S, Sec. 35). At present one fossil deposit is known, and this of rather limited extent. It is situated in a vertical fissure on the east side of the quarry, approximately 2 to 4 feet wide, running from the surface of the limestone downward for about 12 feet. The fissure is filled with a very dark reddish-brown sandy clay. Only one species of snake has been found here: *Crotalus adamanteus.*

Correlation.—I assume this small locality is somewhat equivalent to those at Kanapaha, Arredondo and Reddick I.

Paleoecology.—Unknown.

Reddick I

A limestone quarry approximately one mile south of Reddick, Marion County (R 21 E, T 13 S, SW¼ of NW¼ of Sec. 14), east of U. S. Highway 441; elevation approximately 95 feet. At least two well defined deposits containing vertebrate fossils can be distinguished.

Locality A.—A reddish sandy clay is found in the northern parts of the quarry and fills various fissures and sinkholes. In some places this deposit is fairly consolidated, while in others it is loose. In thickness it varies from 2 to 18 feet, and is overlain by a reddish brown, yellowish brown, or gray sand (Wicomico Terrace sands=(?) Sangamon interglacial (Brodkorb, 1957)). The upper portion of certain parts of this deposit clearly seems to have been truncated, perhaps by an encroaching Pleistocene sea (Sangamon ?). Several fossil turtles were found whose shells were definitely and smoothly sheared off at their junction with the overlying Wicomico Terrace sands. This seems to substantiate the sequential events important in the development of these beds as outlined by Brodkorb (1957). In some places this fossil-bearing bed is clearly shown to rest upon that bed composing the major part of locality B. It thus appears to be younger than that from which the majority of bird and rodent fossils have been taken.

Fauna.—The mammalian fauna from this locality is fairly extensive. Fossil birds are much less numerous than at Locality B. The only species of snakes found in the deposit are: *Elaphe obsoleta* and *Drymarchon corais.*

Paleoecology.—A deposit presumably representing terrestrial conditions; most likely open, dry forest, and possibly similar to that found in the immediate area at the present time.

Correlation.—Presumably younger than Reddick I B.

Locality B.—These beds are best described as the "rodent beds" since these small mammals are remarkably abundant. The deposits collected under this heading show definite bedding planes, and are composed of pinkish, buff, yellow to dark brown sands and clayey sands (Bed 2 of Brodkorb, 1957). One of the most diagnostic features of the deposit is the vast number of fossil vertebrates found. Details of stratigraphy are given by Brodkorb (1957).

Fauna.—This deposit has produced one of the largest Pleistocene faunas yet known from Florida. The list of mammals from this series of beds includes a large number of species, of which approximately 50 percent are extinct. The birds were studied in detail by Brodkorb (1952, 1954b, 1957). Of the reptile and amphibian fossils taken from this deposit there are but a few species missing from a list comprising the known herpetofauna of the central part of the peninsula at the present time. In addition, certain species, such as *Carphophis amoenus* and *Eumeces fasciatus* are at present known only from areas to the north of the fossil locality. The snake fauna includes the following species: *Carphophis amoenus, Diadophis punctatus, Farancia* and/or *Abastor, Rhadinea flavilata, Heterodon platyrhinos, Heterodon simus, Opheodrys aestivus, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Lampropeltis getulus, Elaphe guttuta, Elaphe obsoleta, Pituophis melanoleucus, Tantilla coronata, Storeria* cf. *dekayi. Thamnophis sirtalis, Micrurus fulvius, Sistrurus miliarius, Crotalus adamanteus.*

Correlation.—There is fairly good evidence (Brodkorb, 1957) that this fauna is at least partly equivalent to the deposits at Haile VII, Haile II, and Arredondo I. It is presumed to be Illinoian. Such evidence is found, not only in the similar stratigraphy, but in the identity of certain mammalian, avian and amphibian faunas as well.

Paleoecology.—The large number of bat remains, bones of three cathartid vultures, barn owls, and a swallow, as well as the stratigraphy clearly indicate that this deposit represents a Pleistocene cave. Most important is that several of these birds are represented by bones of individuals too young to fly, as well as by adults (Brodkorb, 1957). The large number of rodents and snakes is attributed to pellets cast by the barn owls.

The smaller vertebrates from this locality represent a wide range in habitat; perhaps a reflection of the wide area covered by the owls in their search for prey. The primary reptilian faunal elements suggest a dry, open forest, but not necessarily scrub. Such conditions exist in the area at the present time. The absence of such aquatic genera as *Natrix* or *Farancia* suggests that there were no ponds close by. Pond dwelling reptiles, such as *Alligator* and *Pseudemys,* though found at Locality B, are uncommon. On the basis of the bird fauna, Brodkorb (1957) suggests that the ecology was that of a wet grassland, or fresh water marsh community. He points out that the fauna indicates that no sizeable body of open water was near, and that the grassland probably was not fed by a permanent stream. These two somewhat divergent views of the paleoecology of the area, both based on a large number of fossils, indicates that considerable additional work must be done before we can hope to obtain a fairly accurate picture of the paleoecology of even one of the best fossil localities in Florida. It should be pointed out, however, that the vast bulk of the bird fossils were obtained from the main bone bed, while most of the snakes were collected from a second locality approximately 260 feet southwest of this area. Possibly the two localities are not contemporaneous, and may represent different ecological conditions. This again points to the need for detailed paleontological research in the complex fissure deposits of the Ocala Limestone.

Williston III

This locality, near Williston, Levy County, was discussed in some detail by Holman (1959).

The snakes reported from the locality include the following forms (after Holman): *Rhadinea flavilata. Diadophis punctatus. Heterodon platyrhinos. Heterodon simus, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Elaphe* sp., *Pituophis melanoleucus, Thamnophis* cf. *sirtalis, Mi-*

crurus fulvius, Agkistrodon piscivorus, Sistrurus miliarius, Crotalus adamanteus.

Eichelberger Cave

A cave west of Belleview, Marion County (R 22 E, T 16 S, Sec. 35); elevation about 90 feet. Fossil vertebrates are known from two localities within the cave.

Locality A.—This deposit is located in the upper level of the cavern. Here the cave earth is redish-brown. The fossils are buff-colored and chalky. There is reason to believe that the northeastern end of this level was open to the surface during the Pleistocene. This is based on some of the fossils themselves, which represent species much too large to pass through the present narrow passageway, and also on the fact that the northeastern end of the upper level apparently is sealed with a mass of limestone boulders and rubble. Here the cavern is close to the surface, and was probably the site of the opening through which the animals passed into the cave.

Fauna.—The only snake known from this deposit is *Coluber constrictor.* Brodkorb (1955) listed the birds from this, and the following locality. *Dasypus bellus, Equus* sp. and *Geochelone* attest to the Pleistocene age of the deposit.

Correlation.—Late Pleistocene ?

Locality B.—This deposit, now fully excavated, was located in a small room near the entrance to the cavern on the lower level. The fossiliferous bed is composed of grayish sands, somewhat cemented together in places. The fossils are buff to dark reddish-brown, and chalky.

Fauna.—The extinct mammalian forms from this deposit point to Late Pleistocene time. The snakes now known from the locality include the following species: *Masticophis flagellum, Elaphe guttata, Pituophis melanoleucus, Heterodon platyrhinos, Crotalus adamanteus, Crotalus giganteus.*

Correlation.—Presumably Late Pleistocene.

Paleoecology.—Both the localities within Eichelberger Cave apparently were laid down under water flowing into the cave from the outside. The fauna suggests a dry, open forested area, similar to but probably more open than that existing in the present area today.

Mefford Cave I, A

A rather extensive cave in the Ocala limestone approximately 1½ miles south of Reddick, Marion County, Florida (R 12 E, T 13 S, S½ Sec. 16), just west of U. S. Highway 441; elevation about 100 feet. As far as is known, Pleistocene fossils occur in only the farthest reaches of the cave, particularly the fissures leading southeastward. Fairly complete extinct animals have been found in a bedded dark brownish sand. Occurring as isolated elements are numerous vertebrae of snakes. The fossils are light buff in color, slightly chalky, little mineralized, and quite fragile.

Fauna.—Besides several extinct mammals and some isolated fragments of birds, the following snakes are known from the deposit: *Carphophis amoenus, Heterodon simus, Heterodon platyrhinos, Diadophis punctatus, Elaphe guttata, Thamnophis sirtalis, Crotalus adamanteus.*

Correlation.—The presence of *Carphophis* in this deposit suggests that it may be contemporaneous with Reddick I B and Arredondo I (Illinoian?).

Paleoecology.—On the basis of the known fauna there is little reason to postulate climatic conditions very different from those existing in the area at the present time, although the presence of *Carphophis* suggests slightly cooler, and perhaps more mesic conditions (Auffenberg, 1958a).

Bradenton Field

Locality A.—This locality was mentioned by Simpson (1930b) as being an important one for fossil mammals. It is located one mile south of the business district of Bradenton, Manatee County, approximately 100 yards east of the Tamiami Trail, in the north bank of a drainage canal (for a stratigraphic section see Simpson, 1930b). The elevation is approximately 27 feet. The fossil reptiles and amphibians collected at the site were obtained from a series of thin laminae of blackish to dark gray-colored sand, containing small balls of grayish clay, with bits of broken shells. The laminae were located in white beach sands, approximately four feet below the surface. The delicacy of preservation is remarkable, for even fish scales are faithfully preserved.

Fauna.—Simpson (1930b) reported on the mammals from this locality. The snakes include: *Natrix sipedon, Natrix cyclopion, Thamnophis sirtalis.*

Correlation.—Wisconsin or Post-Wisconsin?

This deposit most certainly represents a series of thin beds formed very close to the mouth of a creek as it flowed across the Pamlico beach. That this deposit is probably younger than Haile VII, A, or the Arredondo and Reddick localities is suggested by the fact that the *Pseudobranchus* is *striatus*, the form found in peninsular Florida today; and not the extinct species *robustus,* which is known from several Pleistocene localities in Alachua County. It seems unlikely that this deposit is equivalent to Stratum 3 of various coastal localities, since there is no evidence of admixture with more recent faunas. It may, however, be intermediate in age between Stratum 2 and Stratum 3.

Paleoecology.—The preponderance of fresh water forms (mammalian, reptilian, and amphibian) and the beach sands stained with tannic acid are certainly indicative of a stream or pond close to the beach. The small clay balls might be interpreted as the effects of marine erosion on an older Pleistocene deposit, except that it is then difficult to account for the finely preserved, and very fragile fish scales. The most likely answer seems that the deposit represents a small, probably slowly moving stream that flowed over the Pamlico beach. At the present time such streams are common on the Gulf Coast of Florida.

Allen Cave, Lecanto Cave, or Saber Tooth Cave

Approximately one mile northwest of Lecanto, Citrus County; elevation about 100 feet. According to Simpson (1928) the floor and pockets within the cave were filled with a reddish sandy clay from which the fossils were taken by Mr. Walter W. Holmes in 1928 for the American Museum of Natural History. As in most cave deposits, the fossils were chalky.

Fauna.—Simpson (*loc. cit.*) gave an excellent review of the fossils obtained from this cavern. The fossil snakes now known from this locality include (after Holman, 1958, unless indicated) the following forms: *Carphophis amoenus, Heterodon platyrhinos, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Elaphe* sp., *Lampropeltis getulus* (Brattstrom 1953a), *Natrix sipedon, Micrurus fulvius, Agkistrodon piscivorus, Crotalus adamanteus* (Brattstrom, 1954a; Holman, 1958), *Crotalus giganteus* (Brattstrom, 1954a), *Rhadinea flavilata.*

Correlation.—Simpson (1929a, 1929b) suggested that this deposit is, at least in part, contemporaneous with Stratum 2 of Seminole Field. On the other hand, it bears just as many resemblances to Arredondo I (Illinoian?).

Paleoecology (after Simpson, 1928).—The general impression is that the fauna is of a rather limited ecological scope, indicating a wet lowland, with swamps, drier wooded areas, and a few open glades. The fauna does not suggest a spelean habitat. There is no suggestion that the climate differed from that of the same region at the present time. Many of the mammals indicate warm and moist conditions. The snake fauna suggests a similar ecology.

Payne's Prairie

Locality B.—Vertebrate fossils were first collected on the prairie in 1930 while a causeway was being constructed over the low-lying area. The new locality (B) is on the Camp Ranch, at the eastern end of the prairie, approximately 4½ miles south of Gainesville, Alachua County, on the north side of a drainage canal, about 1½ miles east of Highway No. 441 (R 20 E, T 10 S, Sec. 36); elevation about 73 feet. The fossils collected at this site were obtained from spoil along the north bank of the canal.

Fauna.—Aside from the typical Pleistocene assemblage of mammals the collections contain the following snakes: *Drymarchon corais, Elaphe guttata, Coluber constrictor, Natrix cyclopion, Thamnophis sirtalis.*

Correlation.—Late Pleistocene?

Paleoecology.—The fauna from this deposit, with the exception of the extinct mammals, may be expected in the immediate area at the present time; namely, inhabitants of shallow ponds and marshes.

Seminole Field, Stratum 2

Only the fossils derived from one bone bed overlying the marine Pleistocene Anastasia formation (Pamlico time) at several localities in the vincity of Seminole, west of St. Petersburg, Pinellas County, are included in this section. Fossils from Stratum 3 are briefly discussed under "Pleistocene and/or Recent Deposits". Simpson (1929a, 1929b, 1930b) listed the fauna of this deposit. Both Simpson (1929a) and Cooke (1926) gave stratigraphic sections of these deposits. Attention should be drawn to the fact that the Seminole beds are complex, and there is every reason to believe that many of these represent recent reworking of the older beds, which may be Wisconsin, or Post-Wisconsin in age.[5] This has been mentioned by Bullen and Winters (1953), and is the view held by most workers in this area. The elevation is from 20-30 feet.

The snake fauna includes (after Gilmore, 1938 and Brattstrom, 1953a): *Drymarchon corais, Lampropeltis getulus, Lampropeltis doliata, Coluber constrictor, Elaphe obsoleta, Pituophis melanoleucus, Natrix* sp., *Thamnophis* sp., *Farancia abacura* (?), *Agkistrodon piscivorus, Crotalus adamanteus.*

Melbourne Golf Course, Stratum 2

A locality 3 miles west of the center of Melbourne, Brevard County. Gidley (1927), Loomis and Gidley (1926) and Gidley, in Hay (1932) gave the stratigraphy of this deposit. These workers, as well as Simpson (1929a) gave a complete faunal list.

The snakes (after Gilmore, 1938 and Brattstrom, 1953a) include the following species: *Drymarchon corais, Crotalus adamanteus, Coluber constrictor, Lampropeltis getulus.*

As mentioned under Seminole Field, care should be exercised in assigning forms from these deposits to the Pleistocene, since at least Stratum 3 suggests considerable admixture with much more recent faunas.

Vero Beach, Stratum 2

There is very extensive literature on this deposit. The more important papers are by Sellards (1916, 1919, 1937), Simpson (1929a), Cooke (1928, 1941, 1945), Hay (1926, 1923), Gidley (1929a, 1929b) and Weigel (1958). The deposit is located near Vero, St. Lucie County; elevation about 21 feet. Only Statum 2 is included in this section. Stratum 3 is discussed later under "Pleistocene and/or Recent Deposits".

The only snake known from Stratum 2 is *Natrix* sp.

Florida Lime Company, Pit 2

A limestone quarry approximately two miles south of Ocala, Marion County, Florida (R 22 E, T 15 S, Sec. 28); elevation about 84 feet. The known snake fauna consists of *Crotalus adamanteus*, as originally reported by Gilmore (1938).

Winter Beach

This locality is located in a marl pit near Winter Beach, St. Lucie County, (R39E., T32S., S½ of NE¼ Sec. 3), approximately 5.6 miles north of the original Vero locality; elevation about 3 feet. The stratigraphy of the deposit is as follows (after Winters, personal communication):

6. Muck, arenaceous, probably containing mainly mangrove refuse	4 in-1 ft
5. Banded limestone, quartzose and argillaceous sand	3 in-6 in
4. Marl, of fresh water and perhaps in part of brackish origin	5 ft
3. Coquina, much quartz silt and fine sand near the top, becoming relatively quartz-free one foot down	2 ft
2. Marine shell bed	2½ ft
1. Oolitic-looking quartz sand	?

Fauna.—Bed 4, near the top of the marl contains the following invertebrates: *Helisoma, Menetus, Polygyra, Deroceras.* Near the base of Bed 4 the following invertebrates are found: *Euglandina,* and *Anadera.* In addition, the following reptiles (exclusive of the snakes) and amphibians are known from the same zone: *Bufo* sp., *Rana* sp., *Siren lacertina, Anolis carolinensis, Ophisaurus ventralis, Kinosternon* sp. The snakes include: *Coluber constrictor, Farancia* or *Abastor, Natrix sipedon, Liodytes alleni, Thamnophis sirtalis.*

Bed 3 contains the following forms: *Helisoma, Polygyra, Gastrocopta, Heliocodiscus, Strobilops, Donax,* Gomphotheriidae, *Megatherium.*

The dominant elements of Bed 2, a marine stratum, are: *Donax* and *Mulinia.* Many other marine forms are also found in this stratum.

In addition to the above, the following mammals were taken from the spoil banks, and probably originated from near the contact between beds 3 and 4: *Megatherium, Equus, Holmsina, Boreostracon* (?), *Procyon*

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[5] The radiocarbon date of 82 BC ± 90 (Bullen, 1958) is obviously too young for the entire faunal assemblage of the Seminole Field localities, though it points out the fact that mixing has occurred.

lotor, Tapirus veroensis, Tanupolama and *Odocoileus.*

Correlation.—Winters suggested that the sediments and fossils are part of the Silver Bluff Terrace and that the "Pleistocene" mammals persisted in Florida until near the end of Silver Bluff time, perhaps as recently as 4,000 years ago. There are, however, some arguments contrary to this. The fauna is practically identical to that known from definite Pleistocene deposits, and there is no evidence of admixture of faunas, other than the possible Gomphotherid. Winters hypothesis suggests a rather recent period of deposition, and this may be correct. However, until more evidence becomes available it seems best to refer the locality to the Pleistocene on the basis of its contained fauna.

Paleoecology.—The stratigraphy of the deposit apparently suggests a retreating sea, with fresh water, or slightly brackish ponds near the beach and/or mangrove-covered shores. Bed 4 is of much more importance in the present study, since only from this bed have fossil snakes been obtained. The presence of *Deroceras* certainly suggests that at least during certain periods, this pond was entirely fresh water. The fresh water turtles and salamanders point to the same interpretation. The large number of *Anolis carolinensis* suggests a hammock, or at least heavily wooded areas nearby. Similar ecological conditions can be found in a number of areas along both the east and west coasts of Florida, both behind the dunes and behind the mangrove swamps.

D. *Pleistocene and/or Recent Deposits*

Under this heading are gathered all of those deposits for which field data are inadequate, or localities which seem to indicate admixture of fossils of different ages. In no cases are the fossils from these deposits used as the basis for interpretations of faunistic changes, but only to substantiate such interpretations wherever possible. Many of these localities are considered here as at least partly equivalent to Stratum 3 of Vero, Melbourne, Seminole Field and other similar deposits. In all probability this stratum represents recent re-deposition of Pleistocene fossils, along with more recent remains of man and other animals. The conditions for its formation, as well as the somewhat complex stratigraphy of the deposits, makes for uncertainty that a given fossil specimen was not derived from older beds. Where the three strata are found along the coasts, it is frequently impossible to tell from which particular stratum a given fossil originates, since the contact between Stratum 2 and Stratum 3 is sometimes irregular. Unless Stratum 3 is found where Stratum 2 does not occur it will always be extremely difficult to exclude admixture of the faunas. To my knowledge, no such deposit has yet been located in Florida. Stratum 3 seems to occur only if Stratum 2 is present. Stratum 3 is always found along historically old, or Recent stream courses. The problem was admirably discussed by Cooke and Mossom (1929), Cooke (1945), and Simpson (1929a). Bullen and Winters (1953) discussed the age of this stratum at the Seminole Field locality, pointing out the difficulty encountered in complex beds of this type, and suggested the possibility of admixture. Radio carbon dating of material from Seminole Field (82 BC ± 90, Bullen, 1958) indictates that the interpretation of Recent age for Stratum 3 is, in all likelihood, correct. Weigel (1958) discussed the same stratum at Vero in some detail.

A large number of reptiles, birds, and mammals have been termed Pleistocene in the literature that actually came from Stratum 3 of several localities in peninsular Florida. In the present paper reptiles and amphibians reported from this bed have been excluded from the list of the Pleistocene herpetofauna of the state. In certain cases these records will be discussed under particular fossil species.

Snakes reported from Stratum 3 (after Brattstrom) or without precise data as to horizon include (after Hay, 1917; Gilmore, 1938; Brattstrom, 1953a): *Farancia abacura, Coluber constrictor, Drymarchon corais, Lampropeltis getulus, Pituophis melanoleucus, Natrix* sp., *Crotalus adamanteus.*

In addition to Stratum 3 of the Vero, Seminole and Melbourne localities, certain other deposits in Florida must be classified as Pleistocene and/or Recent.

Crystal Springs, Pasco County

A large freshwater spring located in southern Pasco County (R 21 E, T 26 S, Sec. 35); elevation about 70 feet. Fossil vertebrates have been taken from the bed of this spring under conditions similar to those to be described for Itchatucknee Springs.

The only snake reported from this deposit is *Agkistrodon piscivorus* (Brattstrom, 1953a).

Wakulla Springs, Wakulla County

A large freshwater spring located about 4.5 miles west of Wakulla County (R1W, T2S, Sec. 7, unsurv.); elevation approximately 20 feet. A number of fossil vertebrates have been found along the run of this spring in the past, including one, or possible two proboscidian skeletons (Sellards, 1916; Hay, 1923; Simpson, 1929a). Apparently these remains were taken from the reddish clay over which the spring run flows. The snakes reported from this locality are: *Natrix* sp. and *Thamnophis* sp. (Brattstrom, 1953a).

Hornsby Springs, Alachua County

A large freshwater spring located 1.8 miles north of High Springs, and 0.9 miles east of U. S. Highway No. 25 (R 17 E, T 7 S, SW¼ Sec. 27); elevation about 62 feet. Vertebrate fossils have been found both on the bottom of the stream just down from the head spring, and from the cavernous opening of the spring itself. Some of these fossils were obtained from depths greater than 50 feet. The fossils are dark mahogany to black in color and not well mineralized.

The following snakes are known from this locality: *Farancia abacura* (or *Abastor erythrogrammus*), *Natrix sipedon, Natrix taxispilota, Thamnophis sirtalis, Crotalus giganteus.*

From the nature of the fossils and the mode of deposition, likely the fossils were laid down under conditions similar to those existing at the site today. However, the smaller fossils have been shifted around considerably, so that mixing of Pleistocene and Recent faunas has certainly occurred.

Rock Springs, Orange County

This is a spring about 4 miles south of Mt. Plymouth (R 28 E, T 20 S, Sec. 11); elevation about 35 feet. Fossil remains of Pleistocene vertebrates have been taken from the bed of the stream about 100 yards below the head. The stream flows over the limestone facies of the Hawthorne formation and the deposit contains Miocene, Pleistocene, and Recent vertebrates. The list of mammals from this deposit is rather extensive and the material is being studied by Mr. James Gut. Preservation is good. The fossils are buff to light brown in color, rather than black or dark reddish brown as in most fossils collected from stream beds in Florida.

Fossil snakes from this deposit include *Drymarchon corais* and *Crotalus giganteus*. In washing the bottom deposits numerous light gray non-mineralized elements of *Rana* sp. were found. These are probably Recent. The *Drymarchon* and *Crotalus* vertebrae exhibited the same color and degree of mineralization as the extinct mammals.

Wekiwa Springs, Levy County

A large freshwater spring approximately 12 miles southwest of Williston, Levy County (R 17 E, T 13 S, Sec. 33); elevation about 32 feet.

The known vertebrates from this locality include several extinct Pleistocene forms. Only one snake vertebra has been collected from the stream bed. It apparently represents either *Farancia abacura* or *Abastor erythogrammus*. Obvious Pleistocene-Recent admixture has occurred along the stream bottom.

Itchtuckanee Springs, Columbia County

A series of large springs approximately 5 miles northwest of Fort White (R 16 E, T 6 S, W½ Sec. 7); elevation about 70 feet. The fossil snakes taken at this locality have been washed out of the banks and the bed of the Itchtuckanee River and its tributaries which flow in a southerly direction to empty into the Santa Fe River. Although extinct Pleistocene mammals have been found along almost the entire course of the Itchtuckanee River, and along its springfed tributaries, the vast bulk of the fossil snake material has come from four small areas along the upper reaches of the river.

The river and its tributaries provide an excellent opportunity to study the degree and nature of the admixture of Pleistocene and Recent fossils in a stream bed. There are ample undisturbed Pleistocene beds along the banks of the stream, constantly being eroded by the swift current. The present stream is inhabited by many animals and their bones may be seen scattered along almost the entire bed. The water is clear and studies on rate of mineralization and color change could be carried out easily.

Locality A.—This is a small tributary running into the pool of the head spring of Jug, or Blue Spring, which continues to the Itchtuckanee River, a few hundred feet downstream. The smaller tributary heads in a spring depression approximately one-half mile north of Jug Spring. A section along the tributary is given below.

4. A black, highly organic soil .... 6 in - 1 ft
3. A white to gray, soft and loose clay near the water level (this stratum is more or less localized, since it has not been found in exploratory trenches a few hundred yards north) .... 1-2 ft
2. A soft, loose grayish clay containing considerable mineralized remains of vertebrates, as well as leaves, twigs, barks, etc., which in places may be peat-like. There are numerous small cross-bedded lenses of white sand and broken shells .... 2-3 ft
1. Ocala limestone .... ?

A section a few hundred feet down the small tributary and along the west bank of the stream formed by Jug Spring is as follows:

5. A black, highly organic soil at water level .... 1 ft
4. A white to gray, loose and soft clay without fossils .... 1 ft
3. A bedded layer of sand, grayish clay, bits of bark, twigs, etc., and containing some fossils and a vast quantity of broken and eroded *Goniobasis* shells .... 1-1½ ft
2. A fairly homogeneous layer of grayish clay containing many fossils, some *Goniobasis* shells and small pieces of vegetable matter .... 3-8 ft
1. Ocala limestone .... ?

Highly mineralized, black-colored remains of snakes are abundant along the bottom of the tributary and along the stream formed by Jug Springs before it enters the Itchtuckanee River. They have been found in place in Bed 2 of the first section given above, and in beds 2 and 3 in the second section.

A third locality, also containing numerous remains of snakes, is found in the cavernous opening of Jug Spring, from depths of 35 to approximately 60 feet below the surface. Here the vertebrae occasionally are found in place in a freshwater marl at a depth of about 35 feet. The marl bed, approximately one foot thick, overlies a soft orange to reddish clay. Fossil remains are found in both the marl and the clay. The bones are heavily mineralized, and reddish-brown in color; not black, as those found on the bed of the stream near the surface. The remains in this cavern evidently have not been moved too much, since fairly complete turtles and alligators are found imbedded in the marl.

Remains of Recent animals undoubtedly have been washed into the large opening of Jug Spring, but whether they could be carried into the deeper parts of the grotto is unknown. Many limbs and twigs of trees, large, practically pure masses of loose *Goniobasis* shells, and large numbers of mineralized bones of various species of animals, both brown and black in color, are found directly under the shaft-like opening at a depth of 35 feet. In addition, two flint projectile points, some bottles, and a steel gig also were found in this same place. That mixture has occurred, at least directly below the opening, is obvious.

Locality B.—This area, called the "flats" by the local inhabitants, is a place where the Itchtuckanee River broadens considerably, forming a wide, marshy tract, but with deeper channels through which the river flows with considerable current. Some snake vertebrae have been found in this area, as well as remains of many extinct larger vertebrates. A section through the bank of the largest and deepest channel is as follows:

3. A soft brownish, oozy clay silt, at, and slightly above water level, which is apparently Recent in age. This stratum contains bones in varying degrees of mineralization, which display colors ranging from gray to black .... 1-2 ft
2. A fairly loose grayish clay that becomes more compact downwards, containing a considerable number of fossils which are black to reddish-brown in color. Farther down the stream this same bed contained an articulated half of a *Sternotherus* shell, gray in color and showing no indications of mineralization. Just a few inches from this same shell, and also deeply buried in the same matrix was the worn molar tooth of a *Mastodon americanus* .... 7-10 ft

1. A sandy clay to pure sand, grayish to white in color, in which the sand grains have a definite tendency to become cemented together. This bed contains remains of *Mastodon* and *Equus*, etc. The sand is frequently tightly cemented around the bone, and is usually stained a rusty color where it touches it. The fossils from this zone are usually dark gray, brown, or buff in color, and at times may even approach a lavender hue .... 3 ft

The flood plain along the upper reaches of the river is well developed, being level, and a few feet above the surface of the water. On either side of this plain the Ocala limestone is exposed at higher elevations, so that apparently the river may have been much broader at one time. This period of increased flow may, or may not, be correlated with the rise of sea level in Pamlico time. Abandoned stream valleys are sometimes found in the northern part of the peninsula (Edwards, 1949). The soil of the flood plain is highly organic. Under this is found a peat layer, or a loose grayish clay. Both contain twigs and many pieces of mineralized black to dark mahogany-colored bones. These seem to represent re-worked beds, containing fossils derived from older deposits (Bed 1 of the last section given?), as well as containing the remains of animals living in and around the stream at the time of re-deposition. This stratum is Bed 2 of the first, second, and third sections given above. It is intermediate in age between the very recent deposits and the Pleistocene beds exposed in the flats on the bottoms of the deepest holes (Bed 1 of Locality B). Bed 2 contains numerous remains of *Odocoileus*, which are less common in the lower, probably Pleistocene stratum.

Thus, the situation in the Itchtuckanee River is similar to that in many of the coastal localities, where Stratum 3 contains the remains of leaves, twigs, etc., and the remains of Pleistocene vertebrates, and more recent forms, including man. This same stratum also contains remains of deer, and is sometimes termed the "deer zone". Bed 2 of the Itchtuckanee River is probably equivalent to, or nearly contemporaneous with, Stratum 3 of Vero and Seminole Field. Bed 1 of Locality B may be equivalent to Stratum 2 of the coastal localities, which is generally considered to represent a substage of the Wisconsin. As in the coastal deposits the upper fossil-bearing bed contains fossils from the lower bed, as well as a fauna of its own. Unfortunately they cannot be completely separated.

The Itchtuckanee River area and the Vero and Seminole sites are also similar in that modern streams are flowing over the older Pleistocene bed, re-working and re-depositing these fossils. Above this is a Recent soil.

Further work conducted at Itchtuckanee River in a detailed scale, preferably with the mammals, would probably increase our knowledge of the fauna at the close of the Pleistocene considerably.

Fauna.—Simpson (1929a, 1930b) provided a list of the mammals of the Itchtuckanee River complex. In addition, there is a very large avian and herpetological fauna represented in the deposits. Unfortunately, most of the material collected to date was taken from Bed 2. The earlier collections described by Simpson (1939b) were taken from the grayish muck (Bed 2). Lately the majority of the fossils have been found by diving and washing the bottom deposits. The fossil birds from this series of localities are being studied by Mr. John McCoy, Jacksonville University. The snakes now known from this complex series of beds and localities include the following: *Coluber constrictor, Drymarchon corais, Pituophis melaneleucus, Elaphe guttata, Elaphe obsoleta, Lampropeltis getulus, Heterodon platyrhinos, Farancia abacura* (or *Abastor erythrogrammus*), *Natrix sipedon, Natrix cyclopion, Natrix taxispilota, Liodytes alleni, Thamnophis sirtalis, Crotalus adamanteus.*

Paleoecology.—Clearly, much of the material from the river and the various springs represents the fauna of a former stream, probably similar to the present one. However, certain faunal elements strongly suggest a still water environment. This would indicate that perhaps large portions of the stream formed flat, marshy areas, as are now present at the "flats"; or, may indicate that at one time, or several times, the river became ponded, or with flowage reduced to a bare minimum. A thin bed of marsh peat has been found just below the surface in the flood plain of the small stream flowing into the head pool of Jug Spring. It is underlain with a bed representing an old stream channel deposit from which a few fossil bones have been taken. The peat bed may be the stratum from which remains of the pond forms originate.

Haile I

Locality B.—This deposit is located in a lateral fissure 12 feet below the original ground level, at the bottom of a steeply-walled sinkhole, approximately 250 feet north of Locality A. Both deposits are near the edges of an abandoned limestone quarry near the town of Haile, Alachua County (R 17 E, T 9 S, SE¼ of SW¼ Sec. 24); elevation about 84 feet.

The fossil-bearing zone is composed of a thinly bedded gray to reddish-brown sand, containing many small eroded pieces of Ocala limestone. The bones collected from the fissures are buff to grayish in color and not heavily mineralized. Preservation is very delicate.

Fauna.—No extinct vertebrates have been found in this deposit. The snake remains collected from the fossiliferous zone represent the following species: *Coluber constrictor, Drymarchon corais, Thamnophis sirtalis, Sistrurus miliarius, Crotalus adamanteus.*

Correlation.—The relative lack of mineralization and the absence of extinct forms suggests that the locality represents post-Pleistocene time. Both *Sylvilagus floridanus* and *S. palustris* are known from this deposit. The latter is more common than the former. As far as is known, *S. palustris* does not occur in the immediate area today. The species is an inhabitant of marshes and swales. The present conditions in the area of the deposit are almost the opposite; freshwater ponds or lakes being restricted to very small, usually steeply-walled sinkholes. Surface streams are at present absent.

Paleoecology.—Since so few remains are as yet available from this deposit little can be said concerning the conditions during sedimentation. Most of the vertebrates that have been collected from the fossil beds live in the same area today. However, the large numbers of *S. palustris* present in the deposit suggest conditions considerably more moist than those at present.

IV. SKELETAL ELEMENTS AS DIAGNOSTIC MATERIAL IN THE IDENTIFICATION OF FOSSIL SNAKES

Practically all the various elements comprising the skeletons of snakes have been found as fossils. Cranial and mandibular elements, though found only occasionally, are considered by most workers as the most important, though little is known concerning the extent and nature of variation in these elements in modern species. That the skull has been used by many workers in classification, at least of the major categories, is well known. Studies based on comparative morphology of the teeth, cranium, mandible, and even various aspects of the head musculature all assist in identifying fossil snake crania.

Vertebrae and ribs are the commonest remains of fossil snakes. Yet, few studies have dealt with the diagnostic value of these elements as a tool in paleontology. The increasing interest in fossil snakes makes such studies imperative. The only detailed study was that by Johnson (1955), who examined the degree of inter- and intracolumnar variability of vertebrae. Of considerable importance is that he found no correlation between vertebral shape and "modes of existence". Snakes that are related have similar vertebrae, while unrelated types with similar modes of existence have dissimilar vertebrae.

One could argue that the modes of existence assigned to certain species by Johnson are over-simplified. However, the fact remains that interspecific differences in snake vertebrae appear to reflect phyletic relationships.[6] This fact, assumed by earlier workers, was never demonstrated as fully as in Johnson's study. However, as useful as Johnson's paper may be, it does not aid in the identification of vertebrae; it simply suggests that these elements can be used in the identification of snakes, even on the basis of isolated elements.

Individual snake vertebrae are notoriously difficult to identify. This is partly because the degree of individual variability and specific differences have never been investigated thoroughly. Still, these elements have been used in identification of fossil snakes

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[6] Vertebrae of unrelated species may resemble one another, though these similarities are usually superficial, and the basic type is generally easily discernible.

in studies as early as those by de Rochebrunne (1880, 1881) and Owen (1839, 1841, 1849) (notwithstanding Cuvier's remark in 1824 that all non-boids are so similar that they cannot be identified on vertebrae alone). Most of the earlier studies on fossil snakes dealt with these remains on a generic level, though specific names were frequently used. This is evident when one examines the lists of the comparative material available to these workers. Even Johnson's study dealt with variation on a generic level.

Data on ontogenetic, geographic and individual variation in vertebrae of snakes have never been published. In the present paper variational data are given only when they are useful in the identification of species found as fossils in Florida. Until considerably more skeletal material becomes available than is now found in collections, an analysis of vertebral variation, even in only the New World Colubridae, must be deferred.

The study of snake vertebrae has become specialized with a descriptive technique and terminology somewhat different from other branches of paleontology. Unfortunately, usage of some of the terms is variable. Simpson (1933) attempted to standardize this terminology. In some instances subsequent authors misinterpreted certain terms and some useful characters have never been described from a comparative standpoint and deserve names.

The meaning of terms used in this paper is given below. The list has been adapted mainly from Owen (1849, 1852), de Rochebrunne (1881) and Simpson (1933). Emendations are made wherever necessary. Authorities are given only when there is some question regarding the interpretations given by different workers.

Accessory Process: A spine-like process which, if present, projects laterally from just below the prezygapophysial articular facets, and is more or less continuous with the buttress of the prezygapophysial process. It is a term restricted to the snakes, and not to be confused with the *processus accessorius* of Soemmetring (1726), which is synonymous with the mammalian anapophysis of Owen (1852). The term mammillary process is to be restricted to a special low, rounded boss found only in mammalian vertebrae (Gadow, 1933).

Centrum: The actual body of the vertebrae, below the neural canal and between the condyle and the cotyle.

Condyle (or, condylus): The approximately hemispherical posterior articular surface of the centrum.

Cotyle (or, cotylus): The anterior concavity of the centrum, for the reception of the condyle of the preceding vertebra. This is the glenoid cavity of many other authors, a term which should be avoided, unless used in connection with the shoulder girdle.

Diapophysis: A term restricted to the upper member of a pair of rib articulations found on either side of the centrum (see paradiapophysis).

Epizygapophysial Spine: A new term to be restricted to a small spur, present in only some colubrid and crotalid genera, located on the posterior edge of the neural arch, just above the postzygapophysial articular surfaces (= the "spur-like process" of Gilmore, 1938).

Interzygapophysial Ridge: The more-or-less horizontal ridge connecting the pre- and postzygapophysial buttresses (= the "ridge", lateral ridge, or zygapophysial ridge of other authors).

Hypapophysis: A median ventral process (double in the Paleophidae), either spine-like, or sigmoid-shaped, compressed, or bulbous. It is found in the anterior vertebrae of all snakes. In typhlopids, aniliids, boids, xenopeltids, and most colubrids it becomes reduced to a haemal keel of variable shape in the middle and posterior vertebrae. It may be present in a weakly developed condition along the posterior portion of the precaudal vertebral column. The haemal keel may be secondarily well developed in certain colubrid and boid genera, so that it becomes deep and plate-like, as in *Hypsirrhinchus* and perhaps even in the Xenoderminae. A well-developed spine is found throughout the column in some colubrids (Xenoderminae, Natricinae, Acrochordinae and Sibynophiinae), the Elapidae, Hydrophiidae and Crotalidae. The matter is obviously far more complex than one in which the structure can be said to be either present or absent, since in some cases it is surely secondarily derived. Such secondarily derived structures must, however, still be termed a hypapophysis. It is important that in the future authors describe the shape of these structures if they are present, and not simply state that they are, or are not present.

Laminae (= *lames* of de Rochebrunne, 1881; *tectum* of Hoffstetter, 1939): The upper portion of the neural arch, above the interzygapophysial ridges.

Lymphapophyses: Laterally paired ventral processes occurring only in the caudal region.

Neural Arch: The two plates arising from the top of the centrum, surrounding the neural canal, and meeting at the midline. The two dorsal halves of the plates above the interzygapophysial ridges are the laminae, and the two plates below the ridges and in contact with the centrum are the pedicles.

Neural Canal: The canal for the spinal cord.

Neural Spine (= *apopyse épineuse* of de Rochebrunne, 1881, and the *neurapophysis,* at least in part, of many authors): A dorsal process, either present or absent, spine-like or plate-like, arising at the midline of the neural arch.

Paradiapophysis (= *diapophysis* in the broad sense of Owen, 1849, 1852; Simpson, 1933; Gilmore, 1938; *diapophysis* plus *parapophysis* of Hoffstetter, 1939; *tubercles costaux* of de Rochebrunne, 1881; *transverse process* of many authors, and the *synapophysis* of Remane, 1936): A paired process of the sides of the centrum, below the prezygapophysis and near the lip of the cotyle. On the precaudal vertebrae they bear ribs, and on the caudal vertebrae they are variously produced. As pointed out by Remane (1936) and others the term diapophysis is incorrectly used when applied to this structure, since it is obviously composed of two elements; the upper diapophysis, and the lower parapophysis. The term paradiapophysis is more descriptive than Remane's term, synapophysis.

Parapophysis: The lower articular facet, and its body, of each paired rib articulation (paradiapophysis) on both sides of the centrum.

Parapophysial Process (= *parapophysis*, in part, of Hoffstetter, 1939; *apophysis transversus inferieures* of de Rochebrunne, 1881, "projection of diapophysis" of several authors): A small process, present or absent. If present variously developed, extending downwards and forwards from the anteroventral portion of the main body of the parapophysis.

Pedicular Foramen (= nutritive foramen, in part, of other authors): A foramen in the pedicle of each neural arch, variable in position and size.

Postzygapophysis: One of a pair of posterior processes bearing articular facets facing downward for the articulation with the prezygapophysis of the following vertebra.

Prezygapophysis: One of a pair of anterior processes arising from near the junction of the neural arch and the centrum on each side, bearing articular facets facing upward.

Prezygapophysial Buttress: The thickened, ridge-like strengthening structure on the antero-lateral portion of the prezygapophysial process.

Pterapophysis Abel, 1919 (= *flügelfortsëtze* of Janensch, 1906; *aliform process* of Simpson, 1933; Gilmore, 1938 and Hoffstetter, 1939): Restricted to the high, wing-like, or spine-like process found at the posterior portion of the neural arch in the members of the family Paleophidae.

Subcentral Foramen (= nutritive foramen, in part, of previous authors): Paired foramina located on the ventral surface of the centrum on either side of the haemal keel or spine, of variable shape and size.

Subcentral Ridges Gilmore, 1938 (= *lateral ridges* of Hoffstetter, 1939, the "rounded ridge" or "buttress" of Simpson, and the central ridges of other authors): A pair of ridges on the ventro-lateral surface of the centrum, converging posteriorly, running from the diapophysial portion of the paradiapophysis posteriorly toward the condyle.

Subneural Process (= *epapophysis* of Gilmore, 1938, a term which should be restricted to the lateral rib articulations on the inner ridge of the horizontal septum in fishes, according to Remane, 1936): A median ridge, or horizontal spine-like process on the floor of the neural canal.

Zygantrum: A mortise-like depression on the posterior part of the neural arch above the neural canal, articulating with the zygosphene of the following vertebra.

Zygantral Foramen: One of a pair of foramina of variable shape and size, located within the zygantrum, somewhat dorsal and lateral to the zygantral articular surfaces.

Zygosphene: A somewhat wedge-shaped median anterior process from the union of the neural arch above the neural canal, bearing two articular facets facing outward and downward for articulation with the zygantrum of the preceding vertebra.

Of prime importance in the identification of fossil vertebrae is a cognizance of the relative constancy of certain of the vertebral characters, at least in certain parts of the column. Johnson (1955) showed that such constancy definitely occurs. The characters which have been used in this study are listed below, with abbreviations used throughout this publication.

Accessory Processes (ap) — Their shape, extent, direction from above and from the front.

Centrum (c) — Its shape, ridges, processes, length (cl) and width (cw, = naw).

Condylus (co) — Whether it is on a neck or not, oblique or not, its length (col).

Cotyle (ct) — Its shape, height (cth), width (ctw).

Haemal Keel (h) — Its shape, length, position and absence or presence.

Hypapophysis (h) — Its general shape, how far back it projects, and how far forward it can be traced.

Interzygapophysial Ridges — Their general shape and degree of development.

Neural Arch (na) — Its height (nah) its width (naw) and whether or not it is provided with either pterapophyses or epizygapophysial spines.

Neural Canal (nc) — Its general shape, its anterior height (nch) and its greatest width (ncw).

Neural Spine (n) — Its general shape, whether it overhangs posteriorly or anteriorly, or both; whether it is flattened or sharp on its dorsal edge; whether or not it is ornamented on its dorsal edge, and how; its height at the anterior edge (nh), its length along the dorsal edge (nlu) and its shortest length (nls).

Paradiapophysis — Whether or not there are one or two articular facets, their shape and position, whether the paradiapophysial process extends below the centrum, and its shape.

Postzygapophyses (po) — Their general shape, their width (pow), length (pol), the width between the outer edges of the articular facets (po-po), the length from the posterior edge of the postzygapophysis to the anterior edge of the prezygapophysis (po-pr).

Prezygapophyses (pr) — Their general shape, their width from the outer edges of one articular surface to the outer edges of the opposite surface (pr-pr); the shape, length and direction of the accessory processes.

Zygosphene (z) — Its shape from above, from the front, its width (zw), angles of the articular surfaces from the front (z°) and its thickness dorsoventrally (zt).

Figure 1 illustrates the observed variability in the shape of many of the vertebral processes and structures, and gives the descriptive terminology used throughout this paper in referring to particular shapes.

Many ratios have been found of considerable importance in identifying fossil snake vertebrae. The most important of these are

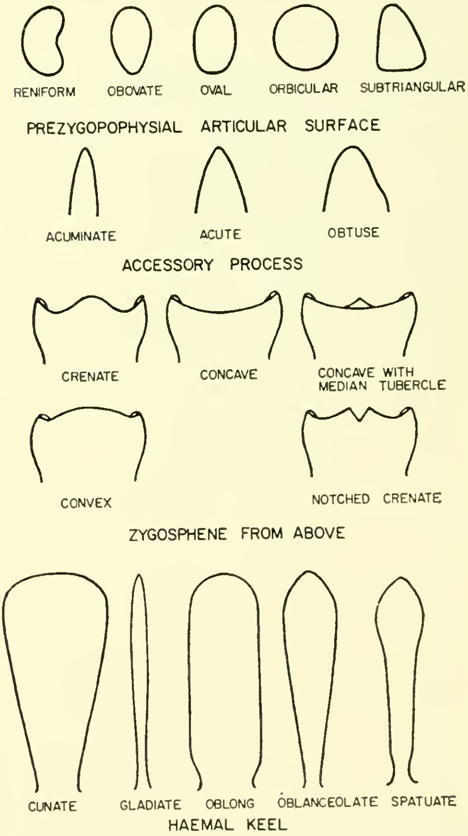


Figure 1. Range of variability in shape of some of the vertebral structures, with the descriptive terms used throughout this paper in referring to shape.

listed below. Others will be found in the diagnoses of certain genera and species.

cl/naw
nlu/nls
naw/po-po
cl/col
nlu/nh
cl/zt
ctw/cth
cl/nlu
zw/naw
nlu/cl
pr-pr/pr-po
zw/cl
cl/zw
pr-pr/naw

Some of the characteristics used in this study to identify fossil vertebrae are constant throughout large numbers of species, distinguishing families and genera; whereas others are confined to particular species. Though there are no well defined vertebral characters to distinguish some genera at the present time, certain species within these closely related genera are sometimes identified easily. This is particularly true in such genera as *Coluber* and *Mastigophis, Lampropeltis* and *Elaphe, Natrix* and *Thamnophis,* etc. Subgeneric categories are frequently recognizable. Subfamilial levels may or may not be evident; and this is sometimes extended even to the family level.[7] In some cases it is possible to distinguish some well differentiated subspecies where these possess definable vertebral types. These and other points will be more fully discussed under the generic and species descriptions.

The foregoing discussion suggests the possibility of utilizing vertebral characters in studying the relationships of the modern species. Such a study is greatly needed, especially with a view towards the determination of higher systematic groupings, at least within the large family Colubridae.

Of all the vertebrae on the column the middle precaudal series (thoracic of some authors) are the most constant in their structure, and are thus best for purposes of identification. However, the isolated nature of most fossil snake vertebrae, and the similarity between middle and posterior precaudal elements introduces a problem which is not always as adequately solved as might be wished. I have based the identification of middle precaudal vertebrae mainly on the relative size of the neural canal. For this reason the middle precaudal vertebrae are discussed at greater length than any others in the descriptions to follow. Unless stated otherwise, all diagnoses, descriptions or tabu-

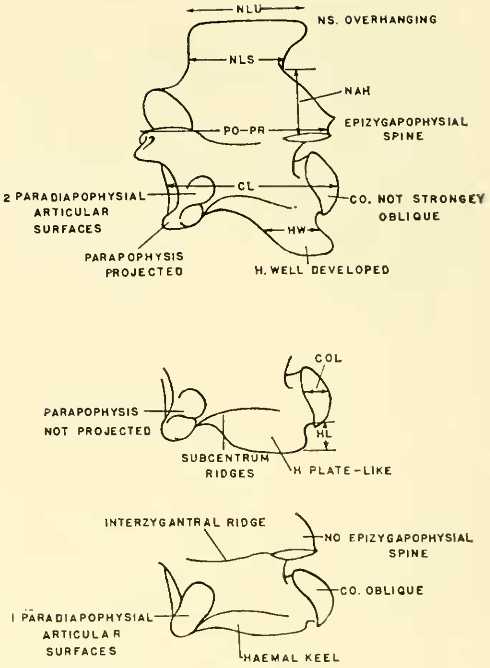
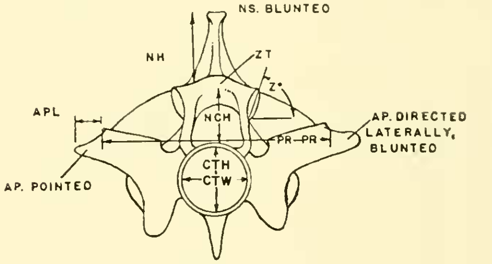
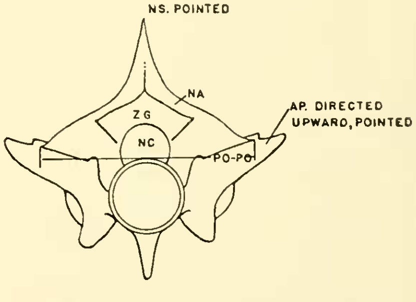


Figure 2. Measurements and terminology used in describing certain vertebral structures, lateral view.



ANTERIOR VIEW



POSTERIOR VIEW

Figure 3. Measurements and terminology used in describing certain vertebral structures, anterior and posterior views.

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[7] Such as the inability to separate the Elapidae and Hydrophiidae, or the anterior vertebrae of certain colubrid and elapid genera.

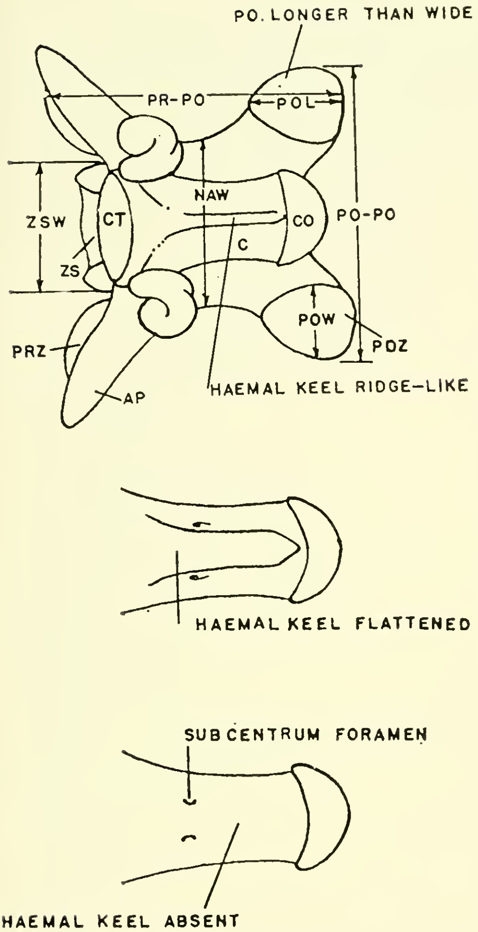

Figure 4. Measurements and terminology used in describing certain vertebral structures, ventral view.

lar data are based on these elements in adult specimens.

Certain measurements were made on both modern and fossil vertebrae so that detailed, objective comparisons could be made. All measurements were taken from single, isolated vertebrae with a micrometer with an altered anvil. In very small vertebrae the measurements were made with an ocular micrometer. Figures 2 to 4 show the various measurements found of some importance in identifying fossil snakes, or in comparing individual vertebrae of extant species of snakes.

V. Taxonomic Descriptions and Discussions

When identification is based on a specialized knowledge, as is required in the present study, it is desirable to include a key to facilitate identification for those less familiar with the characteristics and variability of the organisms involved. The fact that the degree of variability in snake vertebrae is not too well known lessens the value of such a key. Furthermore, there is every reason to believe that additional undescribed species will be found in the Mio-Pliocene of Florida. Inter- and intracolumnar variation is known to be considerable. Vertebral differences between many genera and species are minor. Such factors tend to complicate any key which is produced. Nevertheless, several keys are included below, since I feel the time saved the worker identifying the material justifies whatever faults the keys may be found to contain with further study. The keys are relatively simple and definitive. They should enable the worker to identify all of the described fossil snakes of Florida from Miocene and Pliocene deposits. A key to the Pleistocene snakes is not given, because I feel that the Pleistocene snake fauna of Florida eventually will be found to contain all of the Recent species found in the area, as well as some extra-limital forms. The large number of species which would have to be included and their variability makes such a key unwieldly. At present a key is being devised which will identify any Pleistocene or Recent snake of southeastern United States to generic level. Beyond this the worker will have to turn to Recent comparative material. The following keys are presumably based on middle precaudal vertebrae.

A. Key to the Known Miocene Snakes of Florida

1. Neural spine higher than long; centrum length to 8 mm. .... *Pseudoepicrates stanolseni* (fig. 8, p. 160)

Neural spine as long as, or longer than high; centrum length to 4 mm. .... 2.

2. Centrum long, narrow (cl/naw 1.86 - 1.99); hypapophysial spine extending posteriorly to, or beyond the base of the condylus .... *Paraoxybelis floridanus* (fig. 39, p. 189)

Centrum shorter, wider (cl/naw 0.82-1.25); hypapophysial spine not extending to, or beyond base of condylus, but shorter .... 3.

3\. Neural spine not extending posteriorly to the posterior edge of the laminae of the neural arch; small, centrum length about 2 mm. .... *Anilioides minuatus* (fig. 12, p. 164)

Neural spine extending posteriorly to the posterior edge of the laminae of the neural arch; small to medium, centrum length to 4 mm. .... 4.

4\. Neural spine thickened in cross section and along dorsal edge; small, centrum length about 2 mm. .... *Calamagras floridanus* (fig. 11, p. 162)

Neural spine thin, plate-like, not obviously thickened in cross section, or along dorsal edge; medium in size, centrum length to about 4 mm. .... 5.

5\. No accessory processes, zygosphene straight to concave from the front; cotyle distinctly oval (ctw/cth 1.15-1.36); haemal keel without a notch anteriorly; centrum wider (cl/cw 0.82-0.98) .... *Ogmophis pauperrimus* (fig. 10, p. 160)

Accessory processes well developed; zygosphene convex from the front; cotyle more rounded (ctw/cth 1.04-1.11); haemal keel with a notch anteriorly; centrum narrower (cl/cw 1.25-1.36) .... *Pseudocemophora antiqua* (fig. 36, p. 187)

B. KEY TO THE KNOWN PLIOCENE SNAKES OF FLORIDA

1\. Vertebrae very small, centrum length about 1.5 mm; zygosphene markedly crenate from above .... *Diadophis elinorae* (fig. 18, p. 170)

Vertebrae larger, centrum to 5 mm; zygosphene straight to concave from above .... 2.

2\. Vertebrae relatively small, centrum length about 2.5 mm; neural arch short, wide; prezygapophyses small, oval; neural spine presumably low, long; zygosphene very slightly concave from above and from the front .... *Stilosoma vetustum* (fig. 35, p. 186)

Vertebrae larger, centrum length to 5 mm; neural arch longer, narrower; prezygapophyses larger, oval to subtriangular; neural spine almost as high as long; zygosphene strongly concave from above and either convex or concave from the front .... 3.

3\. Zygosphene concave from the front; prezygapophysial articular surfaces subtriangular; neural arch and spine longer; subcentral ridges moderately developed .... *Heterodon brevis* (fig. 22, p. 174)

Zygosphene convex from the front; prezygapophysial articular surfaces oval or subrectangular; neural arch and spine shorter; subcentral ridges well developed .... *Paleofarancia brevispinosus* (fig. 16, p. 169)

C. *Family Boidae*

1. *Subfamily Boinae*

Description. — Middle vertebrae usually without marked compression or aberrant development of processes; usually with oval cotyle, but frequently rounded; neural spine variable, but usually higher than long, always with a straight anterior edge, frequently thickened, sometimes thinner and plate-like; one paradiapophysial articular surface, sometimes faintly indented medially, hypapophyses present anteriorly, absent posteriorly;[8] haemal keel usually gladiate to oblanceolate, rarely greatly flattened, sometimes almost absent.

This family consists of about 20 extant genera with a wide distribution through the tropical and subtropical parts of the world. However, during parts of the Cenozoic the range of this family embraced portions of even Canada and Patagonia. Their known history extends to at least the Eocene in both the New and Old Worlds.

A large number of Tertiary fossil snakes have been placed in this family. Perhaps some do not belong here. According to Gilmore (1938), "the term Boidae as used paleontologically is much broader and more inclusive than as used by modern herpetologists." There is, however, little reason why this should be true when complete vertebrae

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[8] Except in the genera *Tropidophis* and *Trachyboa* (placed in the subfamily Tropidophiinae by Brongersma (1951), and *Bolyeria* and *Caesarea* (placed in the subfamily Bolyerinae by Hoffstetter (1946), where the middle and posterior vertebrae are provided with hypapophyses. Romer (1956) incorrectly states that *Sanzinia* possesses hypapophyses throughout the column.

are available. The vertebrae of snakes are different from one group to another, and the familial relationships based on individual vertebrae usually are easily demonstrated, at least in modern snakes. However, in fossil vertebrae processes are usually eroded or broken so that the shape of important characters cannot be determined always.

A further difficulty experienced in the case of even the modern members of the family Boidae is that vertebral characters which will hold for all of the genera are difficult to define. This is mainly due to the fact that, based on vertebral elements alone, the family is composed of several groups; reflecting only in part, the current subfamilial distinctions within the family.

A classification of the family Boidae based on vertebral characters is obviously beyond the scope of this paper, though a more detailed study of these characters probably will show that such a classification is possible. The Eryciinae and Bolyerinae are in fact based on vertebral characters.

The fossil boids of Florida obviously represent at least two distinct groups, and perhaps three. *Pseudoepicrates,* a new genus from the Miocene of Florida, apparently is representative of a group including the modern genera *Boa, Constrictor, Epicrates, Eunectes, Sanzinia* and related forms. *Boavus,* a fossil North American Eocene genus, apparently belongs to this group. *Paraepicrates* of the same period is definitely closely related. The vertebrae in all of these genera are relatively short, rarely longer than wide. The cotyle is large, usually oval (at least in all juveniles and in the anterior vertebrae of larger specimens). The condylus is strongly oblique. The neural spine is always short, usually high, and rounded or oval in cross section. The second group represented in fossils from Florida possess vertebrae which are longer (occasionally longer than wide). The cotyle is usually rounded and directed more posteriorly. The neural spine is generally lower, longer, and frequently platelike in cross section. The paradiapophysial articular facets usually are more indented medially, and more projected ventro-anteriorly, but not below the level of the centrum. Both *Calamagras* and *Ogmophis* belong to this group, though the latter possesses some rather distinctive characters. The modern genera *Lichanura* and *Charina* may belong here.

Two genera of boids previously were reported from the Miocene of Florida. These are *Ogmophis* and *Neurodromicus* (Vanzolini, 1952). To these should be added *Calamagras.* In the case of *Neurodromicus* additional comment is necessary.

"*Neurodromicus*"

Cope (1873) described *Neurodromicus dorsalis,* the type species, on the basis of one anterior vertebra from the Oligocene *Oreodon* beds of northeastern Colorado. This genus generally has been placed close to the vipers; Hay (1902) placed it in the Crotalidae, Williston (1925) in the Viperidae, and Gilmore (1938) in the Crotalidae provisionally, awaiting additional material. Vanzolini (1952) placed the genus in the family Boidae on the basis of fossil material from Thomas Farm, Florida. Hoffstetter (1953) stated he thought the type vertebra of *N. dorsalis* represented an anterior thoracic vertebra of a colubrid, possibly even Recent because of its slight mineralization in a deposit where mineralization is usually markedly noticeable. After examining the type I am inclined to agree with Hoffstetter that the specimen is not a fossil, but a Recent vertebra that became mixed with material from the fossiliferous bed.

The type (AMNH 1599) has always been considered an anterior vertebra. This is indicated by the very large neural canal, the high neural arch, the weak accessory processes, the shape of the zygapophysial articular surfaces and the relatively short centrum. The important question is its family relationships.

The cotyle of young boids is oval in shape. With growth this structure becomes more rounded (cth ctw in a very young *Constrictor constrictor* 24 inches long, mean 0.73; in an adult 7½ feet long, mean 0.96). According to Vanzolini the anterior vertebrae of definite boids from Thomas Farm are similar to those of the type of *Neurodromicus.* The most anterior vertebra from this deposit seems to represent a snake about 4 feet long, and the cotyle is decidedly oval. In the type of *Neurodromicus* the cavity is round, yet it represents a smaller specimen. This relationship should be reversed if the type of *Neurodromicus* is a boid.

The anterior vertebrae of elapids, most colubrids, as well as *Sistrurus* and *Agkistro-*

don among the crotalids, have a rounded, rather than an oval cavity.

The type specimen of *Neurodromicus* seems to represent a snake about 3 feet long. Many genera of Colubridae are excluded as possibilities on size alone.

A complete tabulation of the data comparing all the possible snake genera to which *Neurodromicus* might be assigned is of no practical value. It is sufficient to point out that the neural spine length along its base and its height, as well as the ratio of the centrum length divided by neural arch width, exclude all possibilities among the colubrids now inhabiting northeastern Colorado. Comparison of measurements and the resulting ratios of the anterior vertebrae of an adult *Sistrurus catenatus* with those obtained from the type show the closest possible agreement with the 39th vertebra (Table 1). The shape of this element and that of the type are identical. The species has not yet been reported in the immediate area at the present time, though this is apparently very close to the western limits of its range. For those reasons *Neurodromicus dorsalis* is tentatively referred to the synonymy of *Sistrurus catenatus.*

TABLE 1.
Comparison of certain measurements (in mm) and ratios between the type of Neurodromicus dorsalis and the 39th vertebra of an adult Sistrurus catenatus

Measurements and Ratios	*N. dorsalis*	*S. catenatus*
Centrum length (cl)	3.81	3.80
Centrum width (naw)	3.12	3.18
cl/naw	1.22	1.20
Cotyle width (ctw)	1.98	2.16
Cotyle height (cth)	2.01	2.03
ctw/cth	1.00	1.06
Zygosphene width (zw)	2.69	2.74
cl/zw	1.41	1.39
naw/zw	1.16	1.16

However, Vanzolini correctly assigned the fossil remains from the Thomas Farm to the family Boidae. As boids, these snakes cannot be assigned to the genus *Neurodromicus.*

Since no name is available for these boids, the name *Pseudoepicrates* is proposed. In vertebral shape they are approached most closely among Recent boid genera by *Epicrates,* and among fossil genera by *Paraepicrates.*

PSEUDOEPICRATES, *gen. nov.*

Diagnosis.—A Miocene snake representing the subfamily Boinae on the basis of the absence of hypapophyses in the posterior dorsal vertebrae, and the presence of zygosphene-zygantral articulations in the caudal vertebrae. It differs from most members of this subfamily in being smaller and in possessing a longer centrum. From the modern genus *Epicrates* it differs mainly in possessing a higher neural spine. *Eunectes, Boa,* and *Constrictor* have precaudal vertebrae in which the centrum is decidedly shorter. It is distinguished from *Loxocemus* in having a longer centrum, a high neural spine, and a smaller zygosphene. From the modern genera *Charina* and *Lichanura* it differs chiefly in being much larger and in having vertebrae which are shorter in proportion to their length. In addition, the neural spine is shorter and higher in proportion.

From the fossil North American boid, *Boavus,* it is distinguished by its longer centrum and more pronounced subcentral ridges. The fossil genera *Calamagras* and *Ogmophis* are smaller and possess vertebrae with lower, longer neural spines. It differs from *Paleryx* in possessing a longer centrum, and from *Paleopython* and *Gigantophis* in being smaller and in having a longer neural spine along its base. It differs from *Paraepicrates* in having a shorter neural spine along its base.

Genotype. — *Pseudoepicrates stanolseni* (Vanzolini).

Vanzolini (1952) described two species of *Neurodromicus* (*Pseudoepicrates*) from the Thomas Farm Miocene, Gilchrist County, Florida. These are *stanolseni* and *barbouri.* Of the former he had seven available specimens, and of the latter five. Later collections at the same deposit have brought 34 additional specimens to light. Comparison of all of the material now available indicates that only one species is involved. On the basis of page priority *stanolseni* becomes the valid specific name.

Vanzolini distinguished the two species by the following characters: the small tubercle on the lip of the zygosphene, the angle formed by the buttress of the prezygapophyses and the paradiapophyses, the width of the neural arch, the length of the neural spine and the thickness of the zygosphene. Furthermore, the size of the two species is different, *stanolseni* being the smaller. All of these differences are demonstrated easily in the proportional changes associated with ontogeny.

A character given considerable weight in the original description is the shape of the articular surfaces of the prezygapophyses. In *barbouri* these surfaces are more triangular, and have their anterior edges perpendicular to the axis of the centrum. In *stanolseni* the surfaces are more rounded and the anterior edge is not straight and perpendicular to the axis of the centrum. This character is a function of the age of the individual. Older specimens of many species of snakes attain relatively larger and more angular prezygapophysial articular facets than are found in the young. This is particularly true of the boids in general, and is well illustrated in figure 5.

The zygosphene of *barbouri* is thicker than that of *stanolseni*. This is a character that also shows considerable ontogenetic change. Young boids have relatively thin zygosphenes, while adults have these structures very heavily developed. The ontogenetic change in this character in a modern boid is shown in figure 5, and in the available specimens of *P. stanolseni* in figure 6.

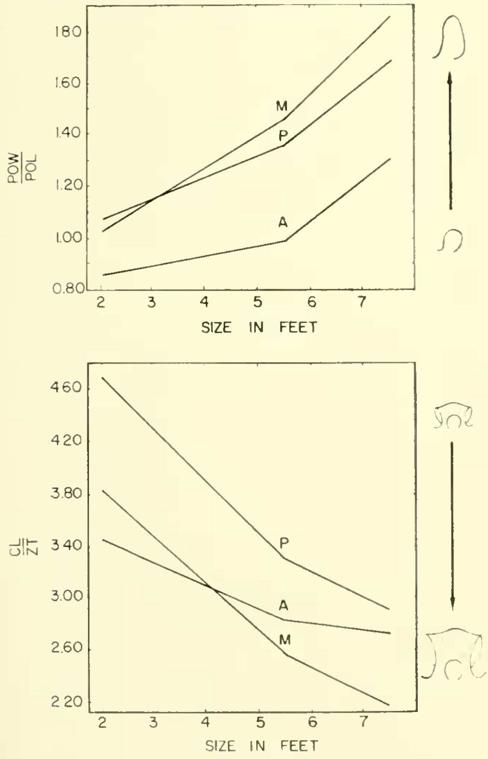

Figure 5. Top: Ontogenetic change in the thickness of the zygosphene. Bottom: Ontogenetic change in the shape of the prezygapophysial articular surface. All data from *Constrictor constrictor*. A = anterior, M = middle, P = posterior precaudal vertebrae.

Young specimens of *Constrictor constrictor* have a neural spine which is very short, while in adults this process becomes relatively longer for its height. The anterior edge of the zygosphene is never provided with a tubercle in young specimens, whereas this structure frequently becomes quite evident in many species with increasing size. Vanzolini stated that the angle formed by the prezygapophysis and the paradiapophysis differs in the two species (p. 456) and referred to his figures 1 and 2. However, such differences are to be expected when comparing vertebrae from the anterior and middle precaudal regions in any snake, even within the same column. The accessory process is usually shorter and directed downward in anterior precaudal vertebrae, whereas it is usually more well-developed, and projected laterally in more posterior vertebrae. He also stated that the height of the neural arch differs in the two species and referred to his figures 8 and 3 Again, such differences are to be expected between anterior and middle precaudal vertebrae.

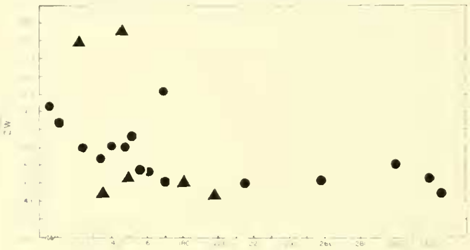

Figure 6. Ontogenetic change in the thickness of the zygosphene of *Pseudoepicrates stanolseni*. Triangles represent vertebrae with hypapophyses, dots represent vertebrae without hypapophyses.

Of the many measurements and ratios which have been gathered from the available specimens of *Pseudoepicrates* from the Thomas Farm, no differences are found which are not easily explained on the basis of ontogenetic change or vertebral position. Furthermore, identical differences can be demonstrated in several species of modern boids when comparisons are made between the ratios of the vertebral characters in different-sized individuals of the same species. Accordingly, *stanolseni* and *barbouri* are here considered conspecific.

Pseudoepicrates stanolseni (Vanzolini)

Diagnosis.—Since this genus, as now known, is monotypic, the specific characters remain those of the genus.

Holotype.—MCZ 1977, an anterior precaudal vertebra.

Type Locality and Horizon.—Thomas Farm, Gilchrist County, Florida, Lower Miocene, Arikareean, Hawthorne formation.

TABLE 2.

Some measurements (in mm) and ratios obtained from the available vertebrae (N = 23) of Pseudoepicrates stanolseni, gen. nov.

cl	2.59-8.66
naw	3.61-10.72
cl/naw	0.68-1.00
pow	1.22-3.51
pol	1.04-4.27
nlu/nh (middle)	0.99-1.32
cth	1.83-5.23
ctw	2.16-5.92
ctw/cth	0.99-1.35
zw	2.08-5.61
nh	1.55-3.79
zw/cl	0.57-0.88
nlu/nh	0.70-1.32
po-pr	4.50-12.19
pr-pr	5.54-15.77
pr-pr/po-pr	1.22-1.29
nlu	1.63-5.26
nls	1.60-4.70
nlu/nh (ant.)	0.70-1.07

It is known only from the type locality, where it is apparently most numerous in the Boulder Bar deposit.

Table 2 shows the variation in certain of the vertebral ratios of this species. Figure 7 shows the intra-columnar variation in vertebral shape based on individual vertebrae which are assumed to come either from one individual, or from a series of specimens of comparable size. Figure 8 illustrates a typical middle precaudal vertebra.

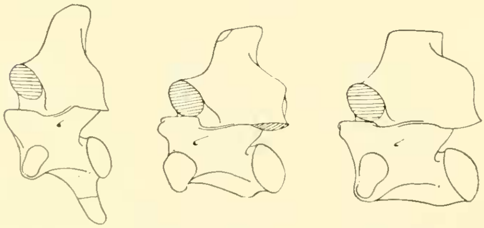

Figure 7. Intracolumnar variation in the vertebrae of *Pseudoepicrates stanolseni.*

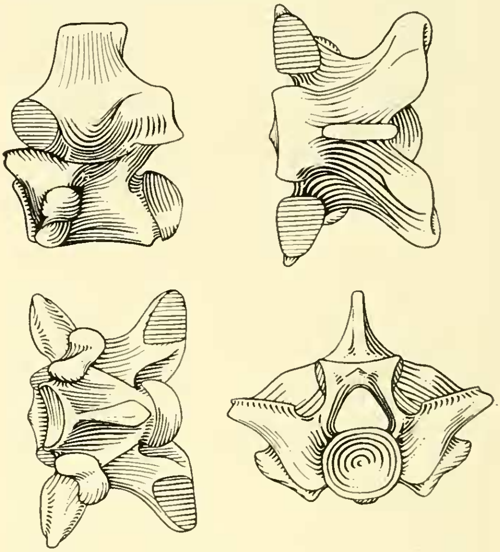

Figure 8. A precaudal vertebra of *Pseudoepicrates stanolseni.*

Ogmophis Cope

Of considerable interest is the fact that Vanzolini described a new species of an apparently semi-fossorial snake, *Ogmophis*, from the Florida Miocene. This genus formerly was known from the Lower Oligocene to Upper Miocene of western United States. A number of additional vertebrae are now available, permitting the original species description by Vanzolini to be supplemented considerably.

Ogmophis pauperrimus Vanzolini

Holotype.—MCZ 1976; a precaudal vertebra.

Type Locality and Horizon.—Thomas Farm, Gilchrist County, Florida, Lower Miocene, Arikareean, Hawthorne formation.

Description (largely after Vanzolini).—Centrum short to moderately long, tapering little, with a distinct pair of subcentral ridges; neural arch flattened, distinctly emarginated between the pre- and postzygapophyses; neural spine low, occupying three-quarters of the length of the neural arch (in middle precaudal vertebrae), reaching a little beyond its posterior margin; zygosphene flat, a little wider than the cotyle, with or without a small tubercle on the anterior surface of the lip, convex to crenate from above, convex from the front; neural canal relatively broad and high, subneural process distinct; prezygapophyses markedly oblique to the midline; zygantrum wide and low; cotyle oval; paradiapophyses auriculiform; condylus slightly oblique with a distinct neck; hypapophyses of middle precaudal vertebrae reduced to a low haemal keel, usually gladiate to oblanceolate, well developed into a ventral spine anteriorly. A typical mid-precaudal vertebra is shown in figure 9.

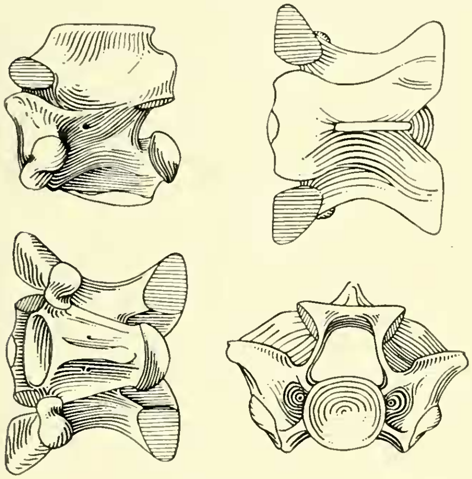

Figure 9. A precaudal vertebra of *Ogmophis pauperrimus* (UF 5131).

In addition to the holotype, 16 vertebrae are now available in the collections of the Museum of Comparative Zoology and the University of Florida. A series of 8 vertebrae from juvenile specimens in the University of Florida collections are also placed in this species. All of the additional material was collected from the Boulder Bar at the type locality.

The additional material allows some comparison of different portions of the vertebral column. These variations are shown in figure 10. Ratios of vertebral measurements are given in Table 3.

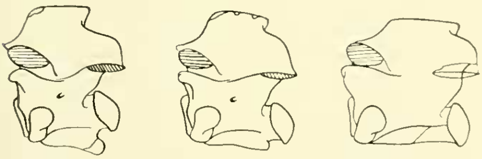

Figure 10. Intracolumnar variation in the vertebrae of *Ogmophis pauperrimus*. From left to right: an anterior precaudal (UF 5137), anterior-middle precaudal (UF 5139), middle precaudal (UF 6312).

TABLE 3.
Measurements (in mm) and ratios obtained from the available specimens (N = 13) of Ogmophis pauperrimus

cl	2.11-3.43
naw	2.13-4.22
cl/naw	0.82-0.98
pow	1.02-1.37
pol	0.89-1.37
pow/pol	0.94-1.20
ctw	1.25-2.69
cth	0.94-2.31
ctw/cth	1.15-1.36
zw	1.80-3.07
zw/cl	0.76-0.91
po-pr	2.36-4.70
pr-pr	4.42-6.45
pr-pr/po-pr	1.38-1.80
nlu	1.09-2.06
nh	4.57-1.05
nlu/nh	1.45-2.52

Remarks.—The genus *Ogmophis* generally has been placed close to *Calamagras*. As originally described by Cope (1873) the two genera are presumably separated by the presence or absence of subcentral ridges extending posteriorly from the diapophyses. However, as Gilmore (1938) pointed out, this character does not separate the two genera satisfactorily.

The type of *Ogmophis* (*oregonensis*) is lost. According to Cope's figure, it is, in many characters, distinct from other species placed in the same genus. Thus the neural spine, which leans forwards and is as high as long, the strong interzygapophysial ridges, etc., separate *O. oregonensis* from *O. arenarum*, *O. compactus* and *O. pauperrimus*. Such differences are of generic level in modern snake vertebrae. Thus there is some doubt that *Ogmophis*, as now recognized, forms a natural group. The presence of one paradiapophysial articular facet, at least in those specimens where it has not been eroded, suggests boid affinities. The type species, *oregonensis*, and *arenarum* definitely have only one articular surface. The surfaces are somewhat eroded in the available specimens of *compactus*, and in most of those of *pauperrimus*. Where they are present, they are somewhat intermediate between a condition which is usually described as either one or two surfaces. Obviously the character is variable in the group currently recognized as the Colubridae; the intermediate condition being uncommon, but certainly present in some genera. *Ogmophis pauperrimus* is similar to *compactus* in possessing two well-defined ridges running from the lateral edges of the glenoid cavity, outward and downward to the paradiapophyses. Such well developed ridges are practically nonexistent in the known fossil boids. As far as is known they are absent in all modern members of this family.

The neural spine is broken off in the only available specimen of *compactus*, but a fairly long spine is suggested by the length of the break itself. In *pauperrimus* the neural spine is longer and lower than in any other boid, with the possible exception of *Epicrates inornatus*. The neural spine in *pauperrimus* is rather thin, not flattened dorsally, and thick as in most boids, including *Epicrates inornatus*. Some of the characters of *O. pauperrimus* are rarely found in the Colubridae, and may even be somewhat characteristic of the anilids. Whether or not *pauperrimus* and *compactus* actually belong in the genus *Ogmophis*, or even among the Boidae is a point which will have to await more complete, and preferably articulated material. It is more probable that they have been placed in the correct family than that they have been placed in the correct genus. The Florida species *pauperrimus* is left in *Ogmophis* for the present.

2. *Subfamily Erycinae*

Calamagras Cope

The genus *Calamagras* appears close to the modern boid genera *Charina* and *Lichanura* (a view apparently shared with Hoffstetter, 1955; Brattstrom, 1958, and Hecht, 1959). This seems indicated by its small size, the tendency for a more elongate centrum, a lower neural spine (generally), a rounded rather than oval cotylus, etc. The vertebrae of *Lichanura roseofusca* show agreement with those of *Calamagras angulatus* in many regards (as has already been indicated by Brattstrom, 1958).

According to Gilmore (1938), the genus *Calamagras* is composed of three species: *murivorus*, *angulatus*, and *talpivorus*. The types of *murivorus* and *talpivorus* were examined during the course of this study.

Calamagras truxalis Cope (1873) was referred to *C. murivorus* Cope (1873) by Cope (1884). Gilmore (1938) followed this arrangement. However, examination of the zygosphene from the front in the types of both species indicates considerable differences; *murivorus* is characterized by a concave zygosphene, while in *truxalis* it is convex. In modern forms differences of this magnitude are generally characteristic of species. Until a fossil column is found in which both conditions are present it seems best to retain *truxalis* as a valid species.

Gilmore (1938) suggested also the possibility that the vertebrae assigned to *C. talpivorus* may really represent more posterior vertebrae of *C. murivorus*. This seems reasonable, since the slight differences which are supposedly characteristic of the two species are demonstrated easily along the vertebral column of almost any modern snake. However, it seems best to retain *talpivorus* as a distinct form until intermediate vertebrae are actually found.

Gilmore (1938) suggested also that *C. angulatus* may represent a different section of the column from which the type of *murivorus* originated, and the former thus may be synonymous with the latter. However, *angulatus* is well distinguished on the basis of a number of characters. *Calamagras primus*, a distinctive species, was described from the Eocene of Wyoming (Hecht, 1959).

In addition to the species mentioned above, known from western United States, two vertebrae have been found at the Thomas Farm which are tentatively placed in this genus. The two specimens are distinct. The first may be known as:

CALAMAGRAS **FLORIDANUS**, *sp. nov.*

Diagnosis.—A small Miocene boid, possessing a short, thick, truncated neural spine, similar to *C. angulatus* in the shape and angle of the interzygapophysial ridge, but differing from that species in the shorter neural spine (nlu/cl—0.56 in *angulatus*) and the sharper hypapophysial, or haemal keel. The short neural spine is found also in *C. talpivorus* (nlu/cl—3.93), but the shape of this structure in the two species is quite different.

Holotype.—UF 6150, collected by Walter Auffenberg, 1954; a middle precaudal vertebra.

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Lower Miocene, Arikareean, Hawthorne formation.

Type Description.—(fig. 11). A somewhat fragmentary precaudal vertebra with the zygosphene missing, and a part of the left postzygapophyses broken. Centrum short, triangular from below, with a median haemal keel, which is gladiate-shaped, not well-defined anteriorly, but extending from the cotyla to the base of the condylus, which is directed posteriorly. The right paradiapophysis is not abraded, possessing one articular facet, parapophysial process faintly projected anteriorly and downward; subcentral ridges present, but not sharply developed, extending from the diapophysis toward the condylus, but not reaching it. Neural arch low, without epizygapophysial spines; postzygapophysis triangular, much wider than long; prezygapophysial processes not projected as an accessory process; neural spine low, short, thick, truncated and thicker on the upper edge; interzygapophysial ridges not parallel to the axis of the centrum, but higher posteriorly, as in *C. angulatus.*

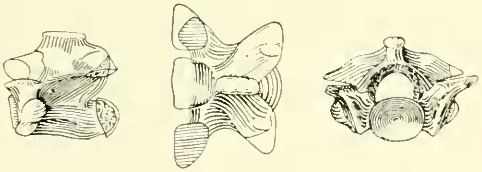

Figure 11. The type vertebra (UF 6150) of *Calamagras floridanus*, sp. nov., Thomas Farm, Gilchrist County. Hawthorne fm., Lower Miocene (Arikareean).

Only one vertebra can be referred clearly to this species. Table 4 gives some of the measurements and ratios obtained from the type specimen.

Figure 13 illustrates the hypothetical relationships of *Calamagras, Ogmophis, Charina, Anilioides,* and *Lichanura.* Brattstrom (1958, pl. 3) suggested a slightly different arrangement. Brattstrom's suggestion that *Cheilophis* is ancestral to this entire group is obviously incorrect in view of the presence of *Calamagras primus* in the Eocene. Furthermore, his view that *Cheilophis* is "questionable" seems unwarranted. The genus seems distinctive. This view apparently is held also by Hecht (1959).

TABLE 4.
Measurements (in mm) and ratios obtained from the type vertebra of Calamagras floridanus

cl	2.49
naw	2.97
cl/naw	0.84
nlu	1.40
nh	0.71
nlu/cl	0.56
nlu/nh	1.96
ctw	2.49
cth	1.35
ctw/cth	1.85

D. *Family Aniliidae*

Description.—Dorsal vertebrae without marked compression or aberrant development of processes; cotyle rounded to oval; neural spine long and low to absent; one or two paradiapophysial articular facets; hypapophyses present anteriorly, absent posteriorly; haemal keel usually greatly flattened, wide, sometimes absent.

The family consists of about 12 genera, though the relationships of most of these are not at all clear, and the family as currently defined (Romer, 1956) may be polyphyletic. Although the vertebral columns of all of the various genera now included in the family have not been studied there is some evidence that three vertebral types are represented in this group. (1) *Loxocemus,* (2) *Xenopeltis,* and (3) *Anilius-Cylindrophis-Uropeltis. Loxocemus* and *Xenopeltis* presently are placed in monotypic subfamilies. Their vertebrae are quite different. Without going into great detail, suffice it to say that *Loxocemus* possesses vertebrae similar to certain genera placed in the Boidae. *Xenopeltis* is transitional between more primitive types and the Colubridae, perhaps through parallel evolution. *Anilius* and *Cylindrophis* possess vertebrae which are basically similar. The neural spine is better developed in the former. *Anilius* is placed in a separate subfamily. *Cylindrophis* and *Uropeltis* are both referred to the Uropeltinae. *Uropeltis* possesses a much longer vertebra. The paradiapophysial articular surface is single, whereas it is double in all of the other genera mentioned above. It is suggested on the basis of vertebral form alone that the Uropeltinae may be polyphyletic. If the familial assignment is retained it may be best to exclude *Cylindrophis* and its close relatives from the Uropeltinae. Either another subfamily should be erected for *Cylindrophis,* etc., or it should be placed with *Anilius.* Before such changes are made the entire group should be restudied and vertebral characters should be considered as well as skull, pelvic and soft anatomy.

ANILIOIDES, *gen. nov.*

Diagnosis.—A small species of Miocene anilid, distinguished from all fossil and Recent members of the family by the presence of a keel on the dorsal surface of the zygosphene, being a continuation of the very short, presumably low, neural spine. In addition, the articular surfaces of the zygosphene project noticeably above the dorsal surface of that element. It differs from *Calamagras floridanus* in the same deposit mainly in not having the interzygapophysial ridge at an angle to the axis of the centrum when viewed from the side, and the neural spine does not extend posteriorly to the edge of the laminae of the neural arch.

Genotype.—*Anilioides minuatus*, sp. nov.

ANILIOIDES **MINUATUS**, *sp. nov.*

Diagnosis.—Sole known member of the genus.

Holotype.—UF 6151, a precaudal vertebra, collected by Walter Auffenberg, 1954.

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Lower Miocene, Arikareean, Hawthorne formation.

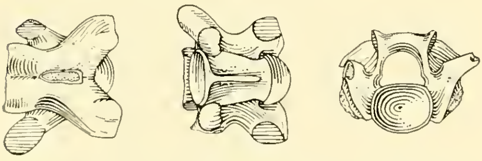

Figure 12. The type vertebra (UF 6151) of *Anilioides minuatus*, sp. nov., Thomas Farm, Gilchrist County. Hawthorne fm., Lower Miocene (Arikareean).

TABLE 5.
Measurements (in mm) and ratios obtained from the type vertebra of Anilioides minuatus

cl	1.96
naw	2.03
cl/naw	1.04
ns along base	1.37
zw	1.37
cl/zw	1.44
ctw	1.27
cth	1.14
ctw/cth	1.11
ns along base/zw	1.00

Type Description.—(fig. 12, table 5). A middle, or possibly posterior, precaudal vertebra. Centrum short, somewhat triangular; subcentral ridges sharp, but diminishing posteriorly, not straight when seen from the side extending from the edge of the cotyle to the base of the condylus; paradiapophyses broken, but apparently with a short, parapophysial projection forwards and downwards; one (?) articular facet. Cotyle rounded; condylus directed upwards. Neural arch short, low, without epizygapophysial spines, with raised portions above the outer edges of the articular surfaces of the zygantrum; with part of the postzygapophyses broken off of both sides. The interzygapophysial ridges are sharp and well-developed. Prezygapophysial articular surfaces oval, the right one broken; zygosphene entire, straight to concave from the front, convex from above with the upper edge of the articular surfaces projected above the level of the lip of the zygosphene. Neural spine broken, but presumably low, definitely long, reaching from the base of the zygosphene to the posterior end of the neural arch, with a slight, but evident keel extending forward to the anterior edge of the zygosphene. A large pedicular foramen, moderate in diameter, is located just above the pedicular-central articulation.

In addition to the type, a more fragmentary, smaller vertebra (UF 5895) is available from the same locality and horizon. The hypapophysial ridge, or haemal keel, is much more developed. The subcentral ridges stand out boldly from the ventral surface of the centrum. The zygosphene is more rounded from the front, and the dorsal keel of the zygosphene is much less evident. In addition, the pedicular foramen is much smaller. The element most certainly represents a posterior precaudal vertebra. Whether it represents this species, or another undescribed form, is unknown at the present time.

Although both of these specimens are small, they do not represent juvenile specimens. This is evident from the proportional size of the neural canal. In juvenile specimens of *Ogmophis pauperrimus* from the same locality the vertebrae themselves are not only longer, but they have proportionately larger neural canals. This is true of all of the juvenile specimens of modern skeletons examined to date. That *Anilioides minuatus* represents an adult specimen, or nearly so, is indicated also by the raised portions of the posterior edge of the neural arch, allowing the zygosphene of the following vertebra to fit into the rather highly placed zygantrum. On the basis of modern comparative skeletons these raised areas occur most often in adults, rarely in juveniles.

The presence of a low neural spine frequently is, though certainly not always, associated with fossorial habits. Presumably *Anilioides, Calamagras,* and at least *Ogmophis pauperrimus*, were semi-fossorial or at least highly secretive forms, as *Charina* and *Lichanura* are at the present time.

E. *Family Colubridae*

Anterior vertebrae always with simple hypapophyses though sometimes modified. Middle and posterior vertebrae either with simple hypapophyses, or the latter reduced to a haemal keel. Accessory processes evident, but of varying lengths. Zygosphene thin, of variable shape. Neural spine always thin, plate-like, never oval in cross section. Cotyle usually round, rarely distinctly oval. Condylus from nearly straight to oblique. Paradiapophyses usually well developed with two articulating surfaces.

If the vertebrae of the Boidae are difficult to identify as fossils, then individual vertebrae of the Colubridae are even more so. Fully three-quarters of the known modern snake genera of the world currently are recognized as belonging to this family. Many forms have become highly specialized and their vertebral form is divergent from one group to the next. Still, vertebral characters are conservative enough so that identification is sometimes difficult, or even impossible in certain cases. This is especially true in species or genera that are close externally.

The vertebrae of a large number of genera and species of modern colubrid snakes have been examined (118 genera, 190 species). Much of the variation in this family pertinent to the identification of the fossils from Florida is discussed under the appropriate form.

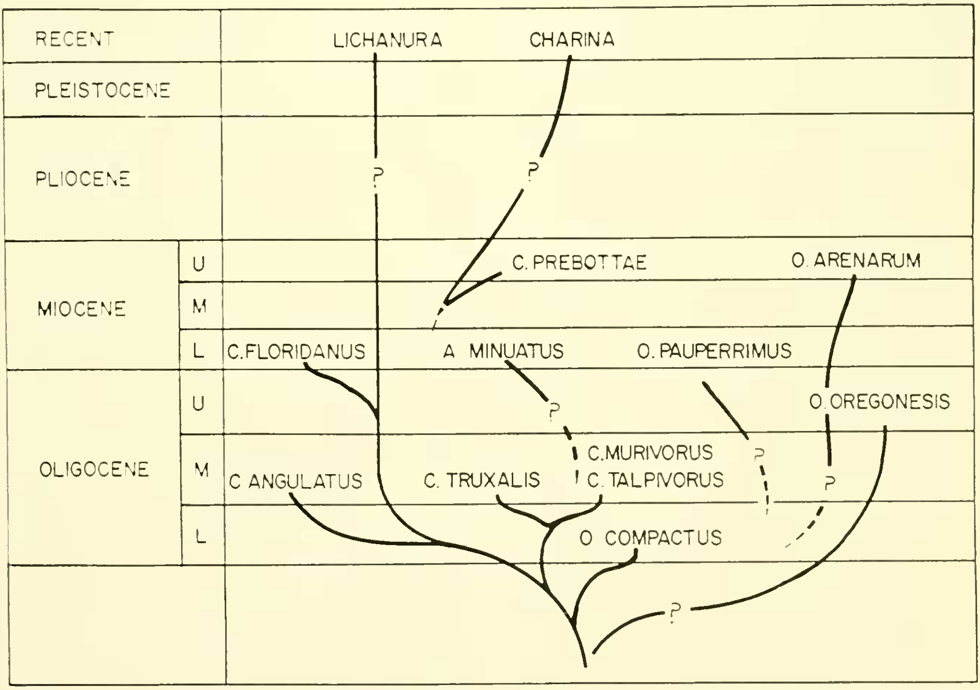

Figure 13. The hypothetical relationships of boids currently placed in the genera *Calamagras* and *Ogmophis,* and *Anilioides*, as well as the possible positions of the Recent genera, *Lichanura* and *Charina.*

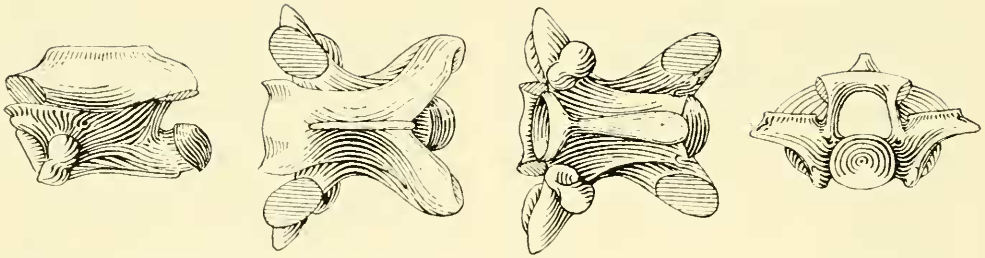

Figure 14. A precaudal vertebra of *Carphophis amoenus* (UF 6141) Reddick I B, Pleistocene (Illinoian ?).

1. *Subfamily Colubrinae*

Hypapophyses reduced to a low haemal keel.[9]

Carphophis amoenus Say

Description.—Typical colubrid vertebrae in which the anterior members are provided with a well developed hypapophysis. Those of the middle and posterior precaudal region are reduced to a low, broad, subspatulate, oblanceolate or cunate-shaped haemal keel, extending from just behind the cotyle to just before the condylus. The centrum is long and narrow, somewhat cylindrical, with fairly well developed subcentrum ridges, extending from the diapophyses at least half way to the condylus, and usually farther. Paradiapophyses with two well defined articular facets, not projecting strongly below and anteriorly. Condylus on a moderately long neck, moderately oblique, slightly to strongly oval. Neural arch long, low, without epizygapophysial spines. Neural spine low, long, occasionally flattened on its dorsal edge, extending forward slightly beyond the base of the zygosphene. Zygosphene crenate from above, convex the front. Prezygapophysial articular surface oval to obovate; accessory process short, acute, flattened dorso-ventrally, directed laterally from above.

The vast majority of the very small vertebrae from the Reddick I deposit can be assigned to this genus. Many vertebrae are provisionally placed here, exhibiting characters very slightly different from those of the modern comparative series. Well over 200 vertebrae are available from the Pleistocene of Florida. That these vertebrae do not represent younger and smaller specimens of larger species is indicated by the neural canal, which is not noticeably enlarged (fig. 14).

A number of modern genera of snakes have been examined and are similar to the fossil form. Genera which have been examined and which may be confused with *Carphophis* when only vertebrae are available are: *Diadophis* (*punctatus,* 4 skeletons examined; *amabilis,* 1 specimen examined), *Sonora* (*episcopa* 1), *Tantilla* (*coronata* 2, *nigriceps* 1, *eiseni* 1), *Enulius* (*flavitorquatus* 1), *Toluca* (*lineatus* 1), *Atractus* (*trilineatus* 1) and *Rhadinea* (*flavilata* 1). Three modern skeletons of *Carphophis amoenus* were examined for intra-columnar variation.

The fossil middle precaudal vertebrae are distinguishable from those of *Diadophis* mainly in having a lower and longer neural spine (nlu nh fossil form, 6.6-8.80; *Diadophis*, 2.2-5.0). In addition, the haemal keel is usually spatulate to cunate in the fossil vertebrae, depending on the amount of flattening, and gladiate to oblanceolate (but keeled) in the latter. From *Tantilla, Carphophis* is distinguished by having much stronger subcentral ridges and a much broader haemal keel, which is gladiate to slightly oblanceolate in the former. From *Toluca* it is distinguished, among other characters, by the convex zygosphene as seen from the top, and by the shorter neural spine, which does not project anteriorly beyond the base of the zygosphene. Differing from *Atractus* by a much wider and more rounded haemal keel. The fossil vertebrae differ from *Rhadinea* by the absence of such well defined subcentral ridges as are found in that genus, by a wider and more rounded haemal keel and by a thicker, shorter and more flattened prezygapophysial accessory process.

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[9] With the exception of certain forms, such as *Ninia* and possibly *Xenophis*, etc. in which these structures appear to have been secondarily developed.

The fossil vertebrae are even more similar to those of *Enulius* and *Sonora*. The fact that the fossil vertebrae obviously belong to a form not present in Florida today is of considerable interest. *Enulius, Sonora* and *Carphophis,* though similar in vertebral structure, reflect entirely different ecological conditions, and thus the determination of the fossil vertebrae takes on additional importance. Of the three genera, *Carphophis* seems the best choice on both ecological and zoogeographical grounds. The vertebrae of these three genera are, however, separable on structural bases, though the differences may be considered slight. *Sonora* differs from the fossils and *Carphophis* in having a shorter centrum (cl/zw 1.00-1.32 in *Sonora,* 1.54-1.88 in the fossil form). However, there are a number of species of *Sonora* which were not available for study, and perhaps some of these have longer centra. *Enulius* apparently differs from the fossils in having a longer neural spine in relation to the width of the zygosphene (nlu/zw 0.89-1.02 in *Enulius,* 1.54-1.88 in the fossil form). In size, and practically all the ratios, the fossil form is similar to the available specimens of *Carphophis amoenus*. There is, however, one character (pr-pr/po-pr) in which a fair proportion of the fossil specimens surpass the lower limits exhibited in the three modern skeletons available for study. The fossil material most certainly represents a much larger number of specimens than were available as modern specimens. The range of variation in this character is somewhat low in the comparative material, yet not exceedingly high in the fossils. The fossil vertebrae are thus assigned to *Carphophis amoenus;* some specimens provisionally until the degree of variability of the pr-pr/po-pr character is fully evaluated. Table 6 compares the ratios obtained from modern and Pleistocene vertebrae.

TABLE 6.
Comparative vertebral ratios in Pleistocene and Recent specimens of Carphophis amoenus

Ratios	Pleistocene (N=51)	Recent (N=38)
cl/naw	1.54-1.88	1.50-1.89
ctw/cth	1.04-1.39	1.08-1.32
pr-pr/po-pr	0.88-1.12	0.96-1.15
po-pr/cl	1.12-1.33	1.15-1.32
nlu/zw	1.20-1.36	1.21-1.46
nlu/nh	6.00-8.80	5.52-7.83
cl/col	4.86-5.82	4.24-5.50
naw/cw	0.88-1.18	0.97-1.17
cl/zw	1.80-2.10	1.86-2.20
pol/pow	1.80-1.92	1.75-2.01

The genus is now known from five Pleistocene localities in Florida: Arredondo I, A (UF 6260, one vertebra), Reddick I, B (UF 5044, 5046, 6141, 6464, 6461, representing many vertebrae), Mefford Cave (UF 2556), and Haile II, B (UF 5778). Holman (1958) reported the genus from Sabertooth, or Lecanto Cave, Florida.

Farancia abacura Holbrook and/or *Abastor erythrogramus* Latreille

The vertebrae of these two genera are difficult, if not impossible to separate, so that the fossil elements from Florida cannot be assigned to one genus or the other with a degree of certainty. On paleoecological evidence there is every reason to believe that both are represented among the fossil vertebrae. The diagnosis given below will apply equally well to both *Farancia* and *Abastor.*

Description.—Anterior vertebrae provided with well developed hypapophyses, which are reduced to a haemal keel in the middle and posterior series. In the middle precaudal vertebrae the haemal keel is oblanceolate to spatulate, whereas it is usually cunate in posterior members. The centrum is subtriangular from below, moderate in length, and provided with strong subcentral ridges from the diapophyses to the condylus. Paradiapophyses well developed, with two articular facets, the diapophysial facet larger and more rounded than the parapophysial member. The parapophysial process is not projected downward or anteriorly. The condylus is fairly large, on a short neck, slightly oblique. The cotyle is rounded, not oval. Neural arch long, low, without epizygapophysial spines. Interzygapophysial ridges prominent, sharp. Neural spine overhanging anteriorly as well as posteriorly, its greatest length equal to, or greater than its height at the anterior edge. Zygosphene concave to straight from above, the same from the front. Prezygapophysial articular surfaces obovate, oval, or subtriangular. Accessory processes directed laterally to slightly downward from the front, laterally from above, obtuse, truncated, and usually flattened.

These genera are similar to some specimens of *Lampropeltis,* especially large adults of the latter. From this genus the former are separable by their more truncated accessory processes, the lower neural arch, which has a thinner zygantral roof and the somewhat lower neural spine.

Hay (1917) reported *Farancia* from Stratum 3 of Vero on the basis of a surangular. Gilmore (1938) questioned the authenticity of Hay's reference of the single element, then no longer available, to *Farancia.* Brattstrom (1953a) reported the presence of this genus in the Seminole Field based on five vertebrae in the American Museum of Natural History (AMNH 7177). I have seen the specimens and agree fully with the determination. Both of these localities are considered here Pleistocene and/or Recent.

A large number of vertebrae, as well as some cranial elements, are now available from additional localities in Florida. These include specimens from the Winter Beach locality (UF 5620) and Reddick I, B (UF 5811). From Itchtuckanee Springs about 40 vertebrae are available from Locality A, most of these coming from the tributary deposit. These are located in the University of Florida Collections. In addition, an occiput (UF 4288) is also available from the same locality. There are two vertebrae (UF 5909, 6263) available from Hornsby Springs. One specimen (UF 9883) was washed out of the cranial cavity of a skull of *Holmesina* from the bottom of Hornsby Springs. A small series of specimens is also available from Jug Springs (UF 5853, 5859, 5886, 5707).

Figure 15 illustrates a middle precaudal vertebrae. Table 7 compares the measurements and ratios of the vertebrae of *Abastor*, *Farancia* and the fossil series from Itchtuckanee Springs.

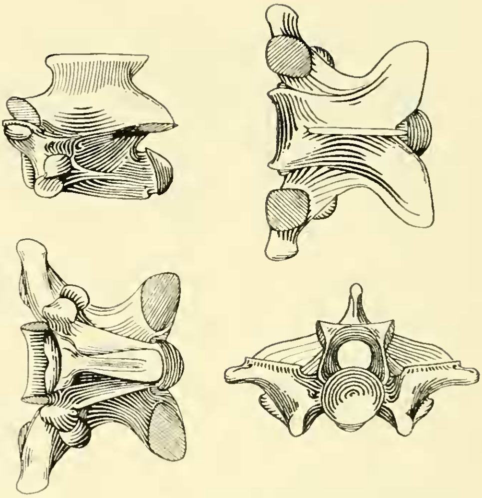

Figure 15. A precaudal vertebra referred to *Farancia* (or *Abastor*) (UF 5359) Itchtuckanee Springs, Pleistocene and/or Recent.

In addition to the remains referred to *Farancia* and/or *Abastor* a single vertebra from Lithia Springs seems close to these two genera, but is provided with characteristics distinct enough to warrant the erection of a new genus.

PALEOFARANCIA, *gen. nov.*

Diagnosis.—A Pliocene (?) colubrid which is apparently related to *Farancia* and *Abastor,* but differing from both in having a higher neural spine, which is less overhanging posteriorly.

Genotype. — *Paleofarancia brevispinosus,* sp. nov.

TABLE 7.

Comparison of vertebral measurements (in mm) and ratios in Farancia abacura, Abastor erythrogramus and the fossil specimens

Measurements and Ratios	*Farancia* (N=61)	*Abastor* (N=33)	*Fossils* (N=138)
cl	5.66- 7.98	5.08-5.33	5.54- 7.75
naw	4.85- 7.80	4.19-4.65	5.11- 7.14
cl/naw	0.91- 1.14	1.01-1.22	1.08- 1.23
pr-pr	8.26-13.72	7.62-7.93	7.75-11.74
po-pr	6.50-10.03	6.17-6.86	6.93- 9.65
pr-pr/po-pr	1.09- 1.29	1.15-1.23	1.12- 1.26
zw	3.43- 5.59	3.35-3.71	3.63- 5.08
cl/zw	1.20- 1.71	1.41-1.58	1.38- 1.63
nlu	2.72- 5.99	3.58-3.96	3.94- 5.11
nls	2.62- 4.42	3.38-3.61	3.25- 4.19
nlu/nls	1.03- 1.42	1.00-1.22	1.05- 1.36
nh	1.55- 4.42	1.52-1.91	1.83- 3.89
nlu/nh	1.75- 2.28	1.78-2.30	2.02- 2.26

PALEOFARANCIA BREVISPINOSUS, *sp. nov.*

Diagnosis.—The specific characters remain unknown since the genus is monotypic.

Holotype.—A single precaudal vertebra collected by Samuel Telford, 1952. UF 5566.

Type Locality and Horizon.—The stream formed by Lithia Springs, Hillsborough County, Florida (R21E, T30S, Sec. 16). Alachua formation (as defined by Sellards, 1914), Middle Pliocene (?), Hemphillian.

Type Description.—A middle precaudal vertebra of a colubrid snake, in which the centrum is subtriangular when seen from below, possessing a well-defined haemal keel, which is thin, high, and somewhat spatulate-shaped. The centrum is moderate in length and provided with strong and well developed subcentral ridges, extending from behind the diapophyses to the base of the condyle, bending inward slightly near the condylus. The paradiapophyses are well developed, not projected, presumably with two articular surfaces, but which have been badly eroded. The condylus is moderate in size, directed posteriorly. The cotyle is round, not oval. The neural arch is moderate in length, without epizygapophysial spines. The interzygapophysial ridges are prominent, but not overly developed. The neural spine overhangs both anteriorly and posteriorly, its greatest length (nlu) slightly greater than its height at the anterior edge. Zygosphene convex from both the front and from above, prezygapophysial articular facets oval in shape. Accessory process broken on the right side, moderately developed on the left, not nearly so truncated as in *Farancia* or *Abastor*, directed slightly downward from the front, laterally from the top. Figure 16 illustrates the type specimen. Table 8 gives the more important measurements and vertebral ratios exhibited in the type.

TABLE 8.
Measurements (in mm) and ratios of the type vertebra of Paleofarancia brevispinosus, gen. nov., sp. nov.

cl	4.13
zw	3.30
pr-pr	7.96
nlu	2.44
naw	4.90
cl/zw	1.25
po-pr	5.53
nh	1.89
cl/naw	0.85
naw/zw	1.48
pr-pr/po-pr	1.44
nlu/nh	1.28

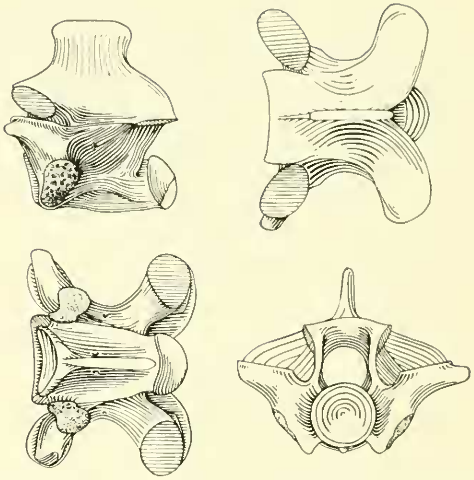

Figure 16. The type vertebra of *Paleofarancia brevispinosus* (UF 5566), gen. nov. et sp., Lithia Springs, Hillsborough County, Middle Pliocene ?.

The relationship of *Paleofarancia brevispinosus* is not clear, though it certainly seems close to both *Farancia* and *Abastor*. No vertebra definitely referrable to either of the modern genera is known from the Pliocene, so possibly *Paleofarancia brevispinosus* is ancestral to one, or both of them.

Diadophis Baird and Girard

Description.—Anterior precaudal vertebrae provided with well developed hypapophyses, which are reduced posteriorly to somewhat rounded haemal carinae, oblanceolate to subspatulate in shape, extending from the cotylus posteriorly to immediately in front of the condylus, ending in an acute point. Centrum subcylindrical to subtriangular, with rounded, usually rather faintly developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus, sometimes less. Parapophyses somewhat projected, paradiapophyses with two articular facets. Condylus moderate in size, directed backward to slightly upward. Cotyle round to slightly oval. Neural arch moderate in length and height, without epizygapophysial spines. Interzygapophysial ridges evident, but not strongly developed. Neural spine long, overhanging posteriorly, and usually anteriorly as well, its greatest length much greater than its height along the anterior edge. Zy-

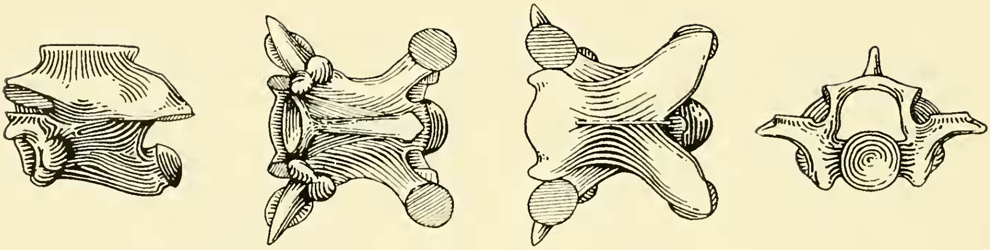

Figure 17. A precaudal vertebra of *Diadophis* cf. *punctatus* (UF 6131) Reddick I B, Pleistocene (Illinoian ?).

gosphene convex from the front, crenate from above (fig. 17).

Skeletons of *Diadophis p. punctatus* (3), *D. p. edwardsi* (1) and *D. amabilis similis* (1) exhibit no constant differences which serve to separate them from one another. Pleistocene remains of this genus from Florida are provisionally referred to *Diadophis punctatus* on zoogeographic grounds. The genus has never before been reported as a fossil.

Diadophis cf. *D. punctatus* Linnaeus

A number of vertebrae provisionally referred to this species are available from Reddick I, B (UF 6131), and Mefford Cave I (UF 2559). They agree in all particulars with those of modern skeletons. Table 9 illustrates the similarity of the ratios of Pleistocene and modern vertebral ratios of *Diadophis punctatus.* Holman (1959) reported this species from Williston, Florida (FGS V-5797).

TABLE 9.
Comparative ratios of Pleistocene and Recent specimens of Diapophis punctatus

Ratios	Pleistocene (N=31)	Recent (N=42)
cl/naw	1.31-1.57	1.23-1.62
ctw/cth	1.11-1.28	1.05-1.38
pr-pr/po-pr	0.96-1.12	0.98-1.16
po-pr/cl	1.15-1.32	1.02-1.44
nlu/nh	3.01-4.86	2.10-5.00
cl/col	4.50-6.09	4.77-6.70
naw/zw	0.90-1.08	0.87-1.11
pol/pow	0.91-1.38	0.08-1.50

In addition to the Pleistocene vertebrae mentioned above, at least two vertebrae are available from a Pliocene locality which are referrable to this genus, and appear to represent a new species. The new form may be known as:

DIADOPHIS **ELINORAE,** *sp. nov.*

Holotype.—UF 6413, a middle precaudal vertebra, collected by Walter Auffenberg.

Type Locality and Horizon.—Haile VI, A, Alachua formation, Middle Pliocene, Hemphillian.

Diagnosis.—A snake whose vertebrae are similar to those of the extant species of *Diadophis*, but which differ from them in having a shorter centrum, in having a straight anterior edge on the neural spine, instead of overhanging anteriorly; in having stronger subcentral ridges; a higher neural spine, and a haemal keel which is less spatulate-shaped.

Type Description.—A middle precaudal vertebra, moderate in length and height, centrum somewhat subtriangular from below. The haemal keel is well developed, slightly rounded, spatulate-shaped, and flattened at the posterior tip where it ends in an acute point, extending from the edge of the cotyle to just in front of the condyle. Subcentral ridges present, but not overly developed, somewhat rounded, extending from the diapophyses posteriorly to little over half way to the condylus, where it disappears. Parapophyses slightly projected downward and forward, the facet of which is smaller than the diapophysial facet. Condylus moderate in size, directed more posteriorly than upwards. Cotyle round, not distinctly oval. Neural arch moderate in length, somewhat compressed dorso-ventrally, but not excessively, without epizygapophysial spines. Interzygapophysial ridges moderate. Neural spine low, straight anteriorly, overhanging posteriorly, longer than high. Zygosphene crenate from above, convex from the front. Prezygapophysial facets oval. Postzygapophysial facets orbicular.

In some respects *Diadophis elinorae* may be confused with *Lampropeltis doliata*, but the neural canal is too small for the centrum length, since it is considerably larger in specimens of *L. doliata* of equal size. From *Chionactis* it differs in that the haemal keel is much narrower, the cotyle is more rounded, and the zygosphene is not as crenate-shaped from above. *Enulius, Sonora, Atractus, Liophis, Toluca,* and *Coronella* also are somewhat similar, but can be separated from the fossil form by a combination of characters involving the shape of the neural spine, the zygosphene, and the width and shape of the haemal keel. For a separation of these and other similar genera, see the section on *Carphophis.*

In addition to the type, two other vertebrae from the same deposit are provisionally placed with it. UF 6153, an anterior vertebra with hypapophysis, and UF 6412, a smaller, somewhat narrower vertebra, is here interpreted as a more posterior element. Figure 18 illustrates the type vertebra as well as one of the referred specimens. Table 10 gives the measurements and ratios obtained from the type.

TABLE 10.

Certain measurements (in mm) and ratios obtained from the type vertebra of Diadophis elinorae, sp. nov.

cl	1.45
naw	1.30
cl/naw	1.12
nlu	1.09
nh	0.25
nlu/nh	4.30
zw	1.24
cl/zw	1.16
ctw	0.79
cth	0.73
ctw/cth	1.07

Rhadinea flavilata Cope

Description.—Centrum long, somewhat cylindrical to subtriangular from below, with well developed hypapophyses anteriorly, reduced to a haemal keel in the middle and posterior vertebrae. Haemal keel low, extending from the cotyle to just in front of the condylus, rounded at its anterior end, flattened posteriorly, compressed laterally near the middle of the length of the keel, oblanceolate to spatulate in shape. Subcentral ridges developed, but not strongly, extending to the condylus. Parapophyses well developed, but not projected. Paradiapophyses with two articular facets, the diapophysial member being larger and more spherical. Condylus on a short neck, moderate in size, slightly oblique, cotyle rounded, not distinctly oval. Neural arch long, moderately low, without epizygapophysial spines. Neural spine long, low, much longer than high at its anterior edge, extending anteriorly beyond the base of the zygosphene. Zygosphene crenate from above, convex from the front. Prezygapophysial articular surface obovate to oval. Accessory processes well developed, acute, directed laterally from the top, laterally to slightly downward from the front, somewhat compressed dorso-ventrally.

Rhadinea flavilata is known from only

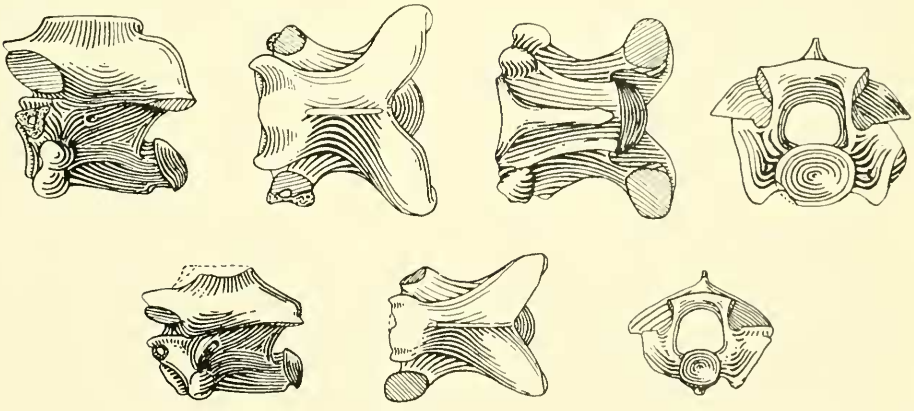

Figure 18. Upper: The type vertebra of *Diadophis elinorae*, sp. nov., (UF 6413), Haile VI A, Alachua fm. (restricted) Middle Pliocene (Hemphillian). Lower: A more posterior vertebra (UF 6412) referred to this species from the same locality.

three localities in Florida: a number of precaudal vertebrae (UF 6134) are available from Reddick I, B. Holman reports it from Sabertooth Cave (1958) and Williston (1959).

In the Reddick deposit this species is most easily confused with *Diadophis* and *Carphophis.* From both it is fairly well distinguished by its stronger subcentral ridges. From the latter it may be separated by its narrower and more ridge-like haemal keel (*cf.* figs. 14, 19). For the characters separating this genus from other similar North American genera, see the section on *Carphophis.* Table 11 compares the ratios of fossil and modern vertebrae of *Rhadinea flavilata.*

Heterodon Latreille

The anterior portion of the column possesses well developed hypapophyses, but they are absent in the middle and posterior series. The haemal keel is somewhat variable, from ridge-like to flattened, gladiate to cunate, extending from just behind the cotyle posteriorly to the edge of the condylus. The centrum is moderate in length and width, somewhat depressed, with subcentral ridges which may be either well developed or weak; if present, extending from the diapophyses posteriorly to near the condylus. Paradiapophyses with two well developed facets. Parapophyses not strongly projected. Condylus on a short neck, moderately oblique. Cotyle round. Neural arch low, depressed, without epizygapophysial spines. Neural spine slightly longer than, or equal to, its height, usually overhanging on the anterior and posterior edges. Zygosphene crenate to convex from above, convex from the front. Accessory process well developed, usually thin and broad, acute to obtuse, usually directed upwards, at least slightly so. Prezygapophysial facets oval to obovate.

On the basis of 8 skeletons of *Heterodon platyrhinos,* 2 *H. simus* and 1 *H. nasicus,* apparently the vertebrae may be separated into two groups: one representing *platyrhinos,* the other the two remaining species. These two groups may be distinguished fairly readily on the basis of the following characters:

(1) Vertebral ratios: pr-po/naw (*platyrhinos* about 2.0, *nasicus* and *simus* about 1.5). The centrum is usually longer in relation to the width in *platyrhinos,* though there is considerable overlap (cl/naw; *platyrhinos* 1.3-1.6 in adults, 1.1-1.2 in hatchlings; *nasicus* and *simus* 0.9-1.4 in adults, no juveniles available).

(2) In *simus* and *nasicus* the ventral keel is flattened to such an extent that it is just about as wide as the ventral portion of the centrum itself. In *platyrhinos* the keel is ridge-like, and not nearly as greatly flattened, except in juveniles.

(3) The vertebrae of *platyrhinos* are generally larger, though this admittedly serves as a character which can be utilized only in certain instances.

Other characters, such as the ratio pr-pr/nah, though they show significant differences in their mean ratios, are considerably more variable, and not suitable for purposes of identification.

TABLE 11.
Comparative ratios of Pleistocene and Recent specimens of Rhadinea flavilata

Ratios	Pleistocene (N=18)	Recent (N=38)
cl/naw	1.42-1.64	1.38-1.54
naw/zw	0.88-1.09	0.97-1.00
cl/zw	1.46-1.65	1.52-1.63
nlu/nh	3.12-4.06	3.14-4.04
pr-pr/po-pr	0.98-1.06	1.00-1.07
po-pr/cl	1.70-2.00	1.73-2.03
cl/col	1.50-1.81	1.57-1.72
pol/pow	0.96-1.16	0.94-1.20

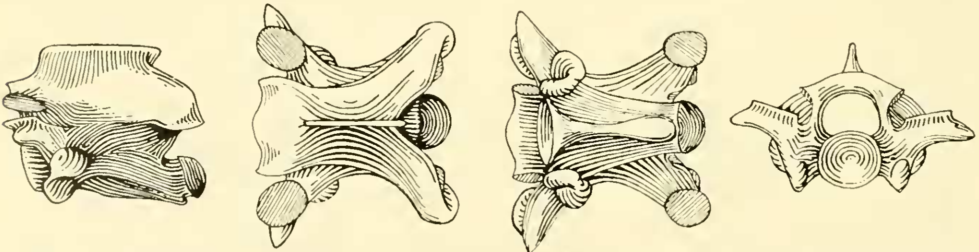

Figure 19. A precaudal vertebra of *Rhadinea flavilata* (UF 6134) Reddick I B, Pleistocene (Illinoian ?).

Heterodon platyrhinos Latreille

This species is now known from the following Pleistocene or Pleistocene and or Recent localities in Florida: Reddick I, B. UF 6134, 6126, 6099, 6046, 6126, 6132, 6049, 6109, 6102, 6107, 6106, 6123, all single dorsal vertebrae; UF 5695, 6 vertebrae, UF 6254, 4 vertebrae, and UF 4312, 3 vertebrae, probably from the same individual. CNHM PR 373. Mefford Cave I. UF 2553, several vertebrae. Haile VII, A. UF 5904, 6330, 5164, 6327, 6323, all single precaudal. Sabertooth Cave, FGS V-5723 (Holman, 1958). Arredondo I, A. UF 6128, one vertebra. Arredondo II, A. UF 2071, 2075, several vertebrae. Eichelberger Cave, B. UF 3331, one precaudal vertebra. Williston, FGS V-5798 (Holman, 1959). Itchtuckanee Springs, A. UF 4390, a complete parietal element, identical in every regard to that of Recent specimens of *H. platyrhinos.*

Figure 20 illustrates a middle precaudal vertebra of this species. Table 12 gives the vertebral ratios of the available fossil and Recent specimens.

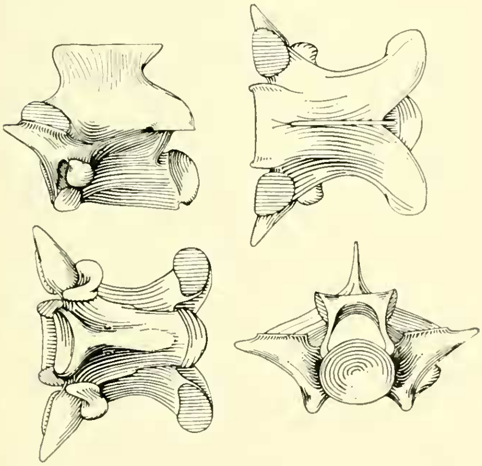

Figure 20. A precaudal vertebra of *Heterodon platyrhinos* (UF 6125) Reddick I B, Pleistocene (Illinoian ?).

Heterodon simus Linnaeus

Heterodon simus has been collected from the following Pleistocene localities: Mefford Cave I. UF 2554, 2 vertebrae. Reddick I, B. UF 5692, 1 vertebra, 5696, 4 vertebrae. Haile VII, A. UF 6213, 1 vertebra. Haile II, A. UF 6032, 1 vertebra. Williston. FGS V-5799 (Holman, 1959).

Figure 21 illustrates a middle precaudal vertebra of this species. Table 12 gives the vertebral ratios of both fossil and Recent specimens of this species.

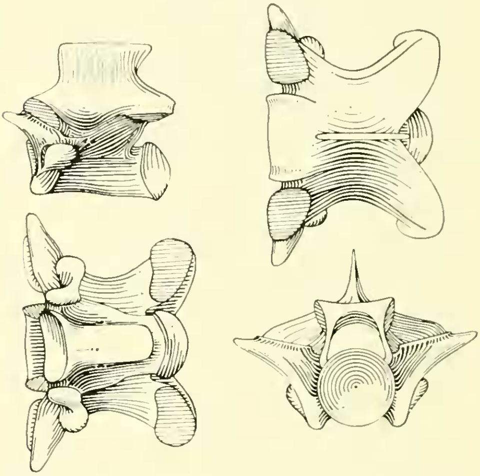

Figure 21. A precaudal vertebra of *Heterodon simus* (UF 5696) Reddick I B, Pleistocene (Illinoian ?).

In addition to the specimens listed above, vertebrae referrable to this genus have been collected from the Pliocene locality of Haile VI. However, these vertebrae are different from either *simus, nasicus,* or *platyrhinos.* The species they represent may be called:

TABLE 12.
A comparison of the vertebral ratios of Recent and fossil Heterodon platyrhinos, H. simus and H. brevis, sp. nov.

	Pleistocene		Recent		Pliocene
Ratios	*platyrhinos* (N=33)	*simus* (N=41)	*platyrhinos* (N=43)	*simus* (N=40)	*brevis*
cl/naw	1.12-1.58	0.92-1.06	1.09-1.62	0.88-1.05	1.19
cth/ctw	0.83-1.00	0.80-0.98	0.81-1.03	0.83-1.00	1.04
pr-pr/po-pr	0.98-1.11	1.08-1.21	0.95-1.18	1.03-1.28	?
zw/naw	0.75-0.87	0.81-0.89	0.73-0.86	0.82-0.92	?
nsl/nah	1.08-1.37	1.06-1.51	1.04-1.41	1.04-1.67	?

HETERODON **BREVIS**, *sp. nov.*

Holotype.—UF 6153, a middle precaudal vertebra collected by Walter Auffenberg.

Type Locality and Horizon.—Haile VI, A, near Haile, Alachua County, Florida. Middle Pliocene, Hemphillian, Alachua formation.

Diagnosis.—A Pliocene species of the genus *Heterodon* in which the middle precaudal vertebrae are similar to those of *H. platyrhinos* in the degree of flattening of the neural arch, with a longer centrum than in *simus* or *nasicus* (cl/naw 1.19), subcentral ridges evident, haemal keel obvious, not as flattened nor as broad as in *simus* or *nasicus*, constricted near the middle. From *platyrhinos* it differs chiefly in possessing a shorter neural spine at its base (cl/nsb 2.07 in the type, 1.32-1.82 in *platyrhinos*). In addition, the prezygapophyses are directed slightly more anteriorly in *brevis*, and the diapophysial facets are proportionately smaller.

Description of Type.—A medium-sized *Heterodon* vertebra from the middle of the column, somewhat fragmentary. The upper portion of the neural spine is broken off. In addition, the right half of the zygosphene and the prezygapophyses on the same side are missing. The condylus is also broken. The zygosphene is slightly concave from above and from the front. There are two articular facets on the paradiapophyses. The zygapophyses are oval. The centrum is provided with two grooves, one on either side of a prominent haemal keel, compressed in the middle, and running from the cotyle, where it is wide, to the condylus, where it is again wide. The keel is not provided with sharp edges, but is somewhat rounded in cross section, not obviously flattened. The cotyle is rounded, slightly higher than wide. The neural canal is somewhat square in outline from the front.

Referred Material.—UF 6466, a fragmental vertebra from the same locality and horizon is provisionally placed in the species. It differs but slightly from the type.

The only other fossil *Heterodon* previously reported is *plionasicus* Peters (1953), a rather large species from the Upper Pliocene of Kansas (Rexroad fm.) (Hibbard 1944, 1949b). This extinct species is most closely related to *H. nasicus*, and is probably ancestral to it. *H. brevis*, on the other hand, is closest to *platyrhinos* and direct phyletic relationship is hardly questionable. Table 12 gives the vertebral ratios of the type. Figure 22 illustrates the type specimen.

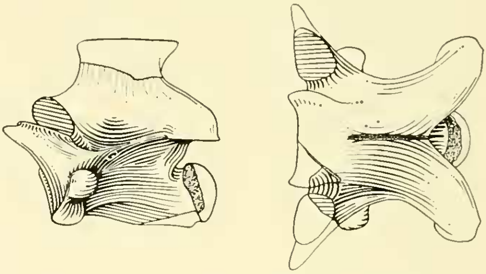

Figure 22. The type vertebra (UF 6153) of *Heterodon brevis*, sp. nov., Haile VI A, Alachua County, Florida. Alachua formation (restricted), Middle Pliocene (Hemphillian).

Opheodrys Fitzinger

Description.—Centrum long, subcylindrical to subtriangular from below, with well developed subcentral ridges, extending from the diapophyses to near the base of the condylus. Condylus on a moderate to long neck, directed more posteriorly than upwards. Haemal keel gladiate to slightly oblanceolate, not spatulate, extending from the lower lip of the cotyle to near the condylus, where it usually ends in an acute point. Paradiapophyses rather small, with two articular facets. Parapophysis not projected ventrally or anteriorly. Neural canal moderate to large. Neural arch without, or with very weakly developed epizygapophysial spines. Zygosphene thin, crenate from above, convex from the front. Neural spine moderate to long, slightly overhanging to straight at the anterior end, overhanging posteriorly.

Opheodrys can be separated from *Coluber* and *Masticophis* on the basis of the height of the neural spine and the width of the zygosphene (nlu/nh: *Opheodrys* 1.39-1.45; *Coluber* 1.77-3.18; *Masticophis* 1.72-2.97; cl/zw: *Opheodrys* 1.20-1.26; *Coluber* 1.41-1.67; *Masticophis* 1.32-1.67). In addition, the haemal keel is not as spatulate in *Opheodrys* as in *Coluber*, but more gladiate-shaped, and usually narrower. The epizygapophysial spines are much less developed than in either *Masticophis* or *Coluber*, and the vertebrae are never as large as in these two genera.

On the other hand, *Opheodrys* is similar to *Salvadora* in vertebral structure. The two genera apparently are separable on the basis of the proportions of the neural spine (nle/nh: *Opheodrys* 1.39-1.45; *Salvadora* 1.54-1.58). In addition, the ratio pr-pr/po-pr will separate many individual vertebrae, but not all of them (*Opheodrys* 0.94-1.01; *Salvadora* 1.00-1.05).

As comparative material of *Salvadora* and *Opheodrys* the following specimens were available: *Opheodrys aestivus* (4), *Opheodrys vernalis* (2), *Salvadora lineata* (1), *Salvadora hexalepis* (1) and *Salvadora mexicanus* (1).

Opheodrys aestivus may be separated from *O. vernalis* by a shorter centrum (cl/naw: *O. aestivus* 1.04-1.07; *O. vernalis* 1.19-1.24), and a longer neural arch (po-pr/pr-pr: 1.07-1.11 in *O. aestivus*, 0.99-1.06 in *O. vernalis*). The remaining ratios and measurements of the two species are practically identical. Both species possess faint, or no epizygapophysial spines. The fossil vertebrae from Florida are clearly referred to *aestivus* on the basis of the two ratios mentioned above.

Opheodrys aestivus Linnaeus

The genus *Opheodrys* has never before been reported as a fossil. Only seven vertebrae are definitely referrable to *O. aestivus*. Two vertebrae (UF 5016 and 6247) are from Reddick I, B. The others are from Arredondo I, A. (UF 6124), Kanapah I. (UF 6184), Haile II, B. (UF 5040 and 5683) and Arredondo II, A. (UF 2072). One of the fossil elements is illustrated in figure 23. Table 13 gives the more important vertebral ratios of the two Recent species, as well as those of the fossil vertebrae.

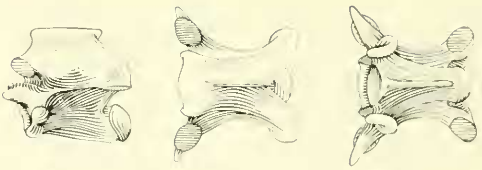

Figure 23. A precaudal vertebra of *Opheodrys aestivus* (UF 6247) Reddick I B, Pleistocene (Illinoian ?).

Coluber Linnaeus

Description.—Middle precaudal vertebrae without well developed hypapophyses; centrum somewhat conical to subtriangular from below, with well developed subcentral ridges. The haemal keel is rounded to somewhat flattened, extending from the lip of the cotyle posteriorly to near the condyle, where it ends in an acute to obtuse point which is usually flattened and broadened, forming a spatulate-shaped haemal keel. The paradiapophyses are provided with two well developed articular facets, with a fairly well developed parapophysial process extending downwards and forwards. The cotyle is suboval to round. The condyle is on a short neck, directed posteriorly. The neural canal is round to subtriangular from the front. The neural arch is moderately long, with well developed epizygapophysial spines. The neural spine is as long, to slightly longer than high, overhanging both anteriorly and posteriorly. The zygosphene is slightly convex from above and from the front. The prezygapophyses are oval to subtriangular, or obovate. The accessory processes are well developed, acuminate, long and directed laterally or slightly downward from the front, and somewhat anteriorly from the top.

The vertebrae of *Coluber* differ from most other elongate colubrids possessing well developed epizygapophysial spines. However, this character seems to have been developed independently several times in both the Colubridae and Viperidae. In the latter they are faintly evident in *Sistrurus* and most specimens of *Agkistrodon*. They are well developed in at least some species of *Vipera*, but are absent in *Crotalus*, *Bothrops*, *Azemiops*, *Bitis*, and *Trimeresurus*. In the New World colubrids they appear to be absent in all of the endemic South and Central American genera which I have seen.

TABLE 13.
Comparison of the vertebral ratios of Opheodrys aestivus, both Pleistocene and Recent, and Opheodrys vernalis

Ratios	*O. aestivus* (N=25)	*O. vernalis* (N=16)	*fossils* (N=32)
cl/naw	1.04-1.07	1.19-1.24	1.04-1.12
nlu/nh	1.39-1.44	1.40-1.45	1.43-1.44
ctw/cth	1.05-1.10	1.06-1.12	1.06-1.08
pr-po/pr-pr	0.99-1.06	1.07-1.11	1.07-1.09
cl/zw	1.20-1.23	1.23-1.26	1.22-1.24

They are weakly developed in *Elaphe,* more strongly in *Pituophis.* They are strongly developed in *Coluber, Masticophis, Drymarchon,* and most of the Natricinae. They are absent, or practically so, in *Opheodrys* and *Salvadora,* two genera sometimes placed close to *Coluber.*

Middle and posterior vertebrae of *Drymarchon* can be separated from both *Coluber* and *Masticophis* by the proportionately shorter centrum, the longer maximum size, the beveled anterior edge of the neural spine and the shape of the haemal keel.

Opheodrys, besides possessing very weak epizygapophysial spines, can also be separated on the basis of other characters from both *Coluber* and *Masticophis.* In *Opheodrys* the neural spine is lower, and the zygosphene is proportionately wider (nlu/nh: *Opheodrys* 1.39-1.45; *Coluber* 1.77-3.18; *Masticophis* 1.72-2.97; cl/zw; *Opheodrys* 1.20-1.26; *Coluber* 1.41-1.67; *Masticophis* 1.32-1.67). *Salvadora* can be separated from *Coluber* and *Masticophis* by the lower neural spine (nlu/nh 1.54-1.58). *Salvadora* usually lacks on epizygapophysial spine.

Other ratios between the four genera are practically identical, or overlap sufficiently so that determination of a single vertebra becomes difficult, if not impossible, on the basis of these characters alone.

The vertebrae of *Coluber* and *Masticophis* are distinct from most other attenuate snakes, including such forms as *Oxybelis, Dryophis, Lygophis, Psammophis, Leptophis, Chlorophis, Alsophis, Dromicus, Uromacer, Immantodes,* and *Leimadophis.*

On the other hand, the vertebrae of the genera *Coluber* and *Masticophis* are similar, and not all specimens of the latter can be separated from the former with any degree of certainty. Brattstrom (1955a: 151-2) separated them on the basis of the smaller size of *Coluber* plus the fact that ". . . the subcentrum keel is narrow, thin and ends anteriorly at the edge of the centrum cup . . . in *C. contrictor,* not thick, flattened, and ending prior to the cup as in *Masticophis.*"

Smaller size is not a particularly good character to separate species (though it must sometimes be used in the absence of the better ones), since younger specimens of snakes can, and do occur as fossils. More important, in eighteen skeletons of *C. constrictor* and nine of *Masticophis* the character concerning the anterior end of the haemal keel will not satisfactorily separate these genera in more than one-third of the total number of vertebrae at hand.

Coluber constrictor frequently has the posterior end of the haemal keel more flattened, and the entire keel is generally thicker. However, this character will not separate more than one-half of the adult specimens, and less than one-third of the younger specimens.

The similarity of these two genera leads to a study of their characters to determine, objectively, the value of some of their vertebral ratios. The best ratio seems to be that of pr-pr/po-pr. There is some suggestion, though slight, of ontogenetic change in this particular character, at least in *Coluber.* This ratio will clearly separate slightly over 65 percent of the specimens of *Masticophis flagellum* and *Coluber constrictor.* However, it will not separate the latter from at least *M. lateralis,* and perhaps other species of *Masticophis.* Based on this ratio, the fossil material from Florida clearly falls into two groups; one certainly representing *Coluber constrictor* and the other *Masticophis flagellum* (fig. 24). Additional vertebrae may be allocated to one genus or the other utilizing the characters mentioned by Brattstrom. However, many of the vertebrae cannot be clearly referred to either genus.

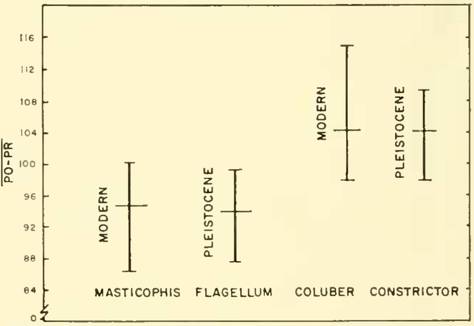

Figure 24. A comparison in the ratio pr-pr/po-pr between Late Pleistocene and Recent specimens of *Coluber constrictor* and *Masticophis flagellum.*

The fact that these two genera are not readily separable on vertebral characters lends another argument in favor of re-uniting the two forms under *Coluber* (Auffenberg, 1956b). All other North American genera known to me are separable on vertebral ratios, with the possible exception of some of the natricines, and some forms of

Elaphe and *Lampropeltis,* and *Farancia* and *Abastor.* There is additional evidence suggesting that the two latter genera should be united.

Comparative material of these two genera available to me for study include: *Coluber c. constrictor* (2), *C. c. stejnegerianus* (1), *C. c. mormon* (1), *C. c. flaviventris* (2), *C. c. priapus* (12), *C. c. paludicolus* (2), *C. c. anthicus* (1), *Masticophis f. flagellum* (6), *M. f. piceus* (1), *M. f. testaceous* (1), *M. lateralis* (1), and *M. taeniatus girardi* (1).

Coluber constrictor Linnaeus

The reader is referred to the generic description of the vertebral character of *Coluber,* since the vertebrae of the two remaining species, *oaxaca* and *spinalis,* are not available for study.

Coluber constrictor is known from a number of Pleistocene and/or Recent deposits in North America. From Florida it was reported from Pleistocene and/or Recent localities (Hay, 1917; Gilmore, 1938; Brattstrom, 1953a; Holman, 1958, 1959). In addition, it is now known from the following Pleistocene localities in the State: Arredondo I, A. UF 6058. Arredondo II, A. UF 2078. Payne's Prairie B. UF 5750. Sabertooth Cave. FGS V-5730 (Holman, 1958). Williston. FGS V-5800 (Holman, 1959). Reddick I, B. UF 5669, 5665, 5667, 5672-4, 5601, 5670, 5572, 5709-12, 5731, 5733-40, 5742-3, 6019, 6045, 6332, 6371, 6456, 9874. Haile VII, A. UF 5188, 5181, 5200, 6328, 5164, 5172, 5840-2, 6195, 9870, 5151-2, 5846-9, 5187, 5179, 5202, 5191, 9884-6, 5176, 5174, 5184, 6307, 5194, 6391, 5157, 5160. Winter Beach Locality. UF 5840. Eichelberger Cave A. UF 5925. Mefford Cave I, A. UF 3512.

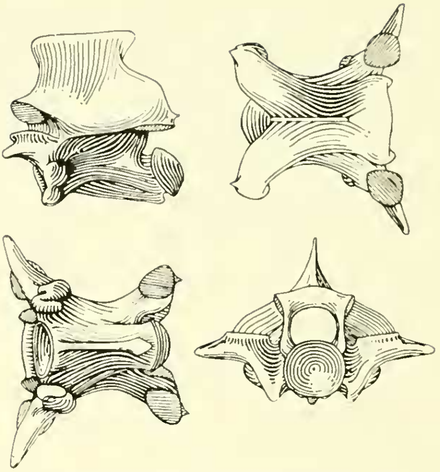

Figure 25. A precaudal vertebra of *Coluber constrictor* (UF 5200) Haile VII A, Pleistocene (Illinoian ?).

A typical precaudal vertebra is illustrated in Figure 25. Table 14 compares the various vertebral ratios of modern and Pleistocene *Coluber constrictor* and *Masticophis flagellum.* Fossil records of *Coluber* from Europe probably should be referred to *Zamenis,* or some closely related genus. The Pliocene specimens referred to this species by Brattstrom (1955a) should be re-examined carefully, since, after examining these vertebrae, I am reasonably certain that not all of them belong to the genus *Coluber.*

Masticophis flagellum Shaw

Description.—Middle precaudal vertebrae without well developed hypapophyses; centrum somewhat conical to subtriangular, with well developed subcentral ridges. The haemal keel is rounded to somewhat flattened, extending from the lip of the glenoid cavity posteriorly to near the condyle, where it ends in an acute point, which is not usually flattened or overly broadened, but gladiate-shaped, and ridge-like. The paradiapophyses are provided with two well developed ar-

TABLE 14.
A comparison of some of the vertebral ratios of Coluber constrictor and Masticophis flagellum, both Pleistocene and Recent

	Coluber		*Masticophis*	
Ratios	Pleistocene (N=51)	Recent (N=45)	Pleistocene (N=36)	Recent (N=41)
cl/naw	1.32-1.48	1.23-1.53	1.42-1.53	1.34-1.64
ctw/cth	0.96-1.08	0.90-1.16	1.01-1.09	1.00-1.18
pr-pr/po-pr	1.03-1.07	0.98-1.25	0.92-0.98	0.87-1.00
cl/zw	1.33-1.60	1.26-1.67	1.40-1.59	1.38-1.76
zw/naw	0.93-1.05	0.89-1.18	0.97-1.09	0.94-1.16
nlu/nh	2.45-3.18	1.86-3.46	2.20-2.63	1.93-2.97
nlu/nls	1.13-1.21	1.09-1.33	1.11-1.21	1.09-1.28

ticular facets, with a fairly well developed parapophysial process extending downwards and forwards. The cotyle is rounded. The condylus is on a short neck, directed posteriorly. The neural canal is round to subtriangular from the front. The neural arch is long, with well developed epizygapophysial spines. The neural spine is long, to slightly longer than high, overhanging both anteriorly and posteriorly. The zygosphene is slightly convex from above and from the front. The prezygapophyses are oval to obovate. The accessory processes are well developed, acuminate, long, and directed anteriorly from above, laterally from the front.

The vertebrae of *Masticophis* can usually be separated from *Coluber*. These differences are discussed in the section dealing with *Coluber*.

Masticophis flagellum is known from the following Pleistocene localities in the State: Arredondo I, A. UF 6141. Haile I, A. UF 5494. Haile VII, A. UF 6303-4, 6392, 5903. Reddick I, B. UF 5713-5, 5720-5, 5728, 5571, 5574, 5634, 5671, 5678, 6014, 6048, 4068, 6351-2, 6368, 8404, 6408, 6475-6. Sabertooth Cave. FGS V-5727 (Holman, 1958). Eichelberger Cave B. UF 6160. Williston. FGS V-5801 (Holman, 1959).

In addition, it is known from Itchtuckanee Springs (UF 5708, 5368), a locality listed in this paper as representing Pleistocene and/or Recent deposits.

A mid-precaudal vertebra of this form is shown in Figure 26. Table 14 compares the various vertebral ratios of modern and Pleistocene vertebrae of *Coluber constrictor* and *Masticophis flagellum.*

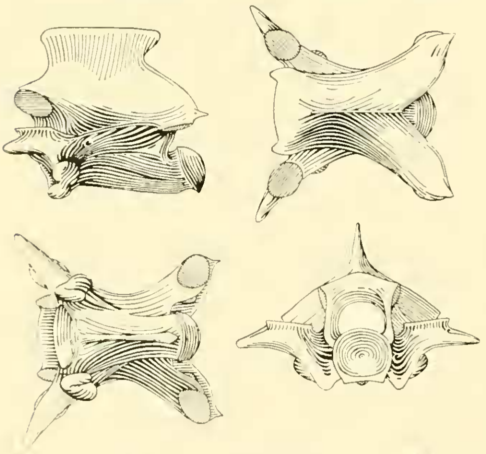

Figure 26. A precaudal vertebra of *Masticophis flagellum* (UF 5722) Reddick I B, Pleistocene (Illinoian ?).

Drymarchon corais Holbrook

Description.—Middle precaudal vertebrae without hypapophyses. Centrum triangular to subtriangular from below, with well developed subcentral ridges, and a rounded or flattened haemal keel, extending from the edge of the cotyle to near the condylus. It ends in an obtuse, or acute, flattened point, directly anterior to the condylus. The haemal keel is frequently thickened laterally near its middle. The cotyle is round, with or without a straight, lower margin, forming two latero-ventral corners. The paradiapophysial articular facets are double, with a parapophysial process extending downward and outward, as well as slightly anteriorly. Although usually present, this process is never overly developed. The condylus is on a short neck, and is directed more posteriorly than dorsally. The neural arch is moderate in length and height, with well developed epizygapophysial spines. The neural canal is rounded to square. The zygapophysial articular facets are oval to obovate in outline. The accessory processes are well developed, acute to broadly obtuse, directed laterally both from the front and from above. The zygosphene is straight above, occasionally notched, or even with a median tubercle in large adults, straight to convex from the front.

The following comparative material of this genus has been examined: *D. corais melanurus* (1), *D. c. erebennus* (2), *D. c. couperi* (6).

The vertebrae of this genus are easily recognized and can be assigned with certainty if they are not broken. In appearance they are typical colubrid vertebrae in which the neural spine is particularly distinctive. It is slightly longer than high, overhanging posteriorly, and with a beveled edge anteriorly. Apparently this is the only genus of snake in the New World with this peculiar anterior edge of the neural spine, with the possible exception of very large specimens of *Drymobius*. From this genus *Drymarchon* may be separated by its lower neural spine (nlu/nh: *Drymarchon* 0.93-1.51, *Drymobius* 2.14-2.53), more obviously beveled neural spine in specimens of the same size, and generally less accentuated epizygapophysial spines. Other differences of lesser significance are seen on direct comparison of the vertebrae of the two genera, though the above will serve to separate them.

When the neural spine is broken difficulty is experienced in separating *Drymarchon* vertebrae from large specimens of *Coluber* or *Masticophis*, especially the latter. The centra of the last two genera are narrower and longer (cl/naw: *Drymarchon* 0.85-1.30 [M = 1.21], *Masticophis* 1.03-3.59 [M = 2.36] and *Coluber* 1.92-3.50 [M = 2.52]. The accessory processes are heavy, but pointed in *Drymarchon*, whereas they are usually more acute in larger specimens of *Masticophis*, and in some specimens of *Coluber*. Small specimens of the last two genera easily are told from *Drymarchon* in a number of characters. The haemal keel is thinner in *Masticophis* and *Coluber*. The vertebrae of *Spilotes* also are somewhat similar to those of *Drymarchon* and may be distinguished by the width of the zygosphene, which is as wide as the narrowest part of the neural arch in *Spilotes*, and narrower in *Drymarchon*. In addition, the shape of the neural spine is different, the beveled edge being absent in *Spilotes*.

Drymarchon is known in the fossil record only from the Pleistocene of Florida. In addition, it has been reported from a number of localities in the peninsula that are here regarded as Pleistocene and/or Recent.

Gilmore (1938: 66) mentioned that the fossil remains of this snake are identical to those of modern specimens with one exception: "The hypapophysial keel in many of the Pleistocene vertebrae has flattened ventral surfaces, whereas it is rounded in the skeleton of the living form . . . [and] (p. 64) the extinct form . . . probably . . . represents a distinct species . . ." The most careful examination of the vertebrae of both modern and Pleistocene specimens shows that the flattened keel is by no means restricted to fossil specimens, but is found in larger modern skeletons as well, and is a result of ontogenetic development.

One excellent fossil specimen of *Drymarchon* was found in the Pleistocene of Florida (UF 5076), including 52 vertebrae from all portions of the body, as well as certain of the cranial elements. When this specimen is compared with a large modern skeleton of this species the closest agreement is found in both the vertebrae and the cranial elements. However, certain vertebral ratios are significantly different in the two forms. These differences have their bases in the ontogenetic development of the vertebral elements, and are not necessarily indicative of a distinct species or subspecies (fig. 27). From all available data this fossil specimen seems to have been about 8-9 feet long, only slightly, if at all, larger than modern specimens. When Pleistocene vertebrae are compared with modern vertebrae of the same centrum length, the ratios are not significantly different. In view of the above, the Pleistocene remains of *Drymarchon* are referred to the Recent species, *corais*.

Because of its large size, this species is one of the most common fossil snakes in collections. Well over 200 vertebrae are known from Florida. However, almost all of these were found in localities here listed as Pleistocene and/or Recent. The species is known from the following Pleistocene localities: Arredondo I, A. UF 5009-10, 5076. Arredondo I, E. UF 5901. Reddick I, B. UF 6071-2, 5011, 6011, 5014, 5012, 5575, 6364, 6492, 5805, 6491, 6369, 5263, 5716, 6350, 5915, 6015, 5635, 6142, 5602, 5916, 5107, 6353, 5467, 6036. Haile VII, A. UF 5205, 6208, 6283, 6277, 6292, 6301, 9864, 9868. Haile IV, A. UF 6022. Haile I, A. UF 5463, 5920. Kanapaha I. UF 5746. Winter Beach. UF 9872, 9882. Payne's Prairie B. UF 6488, 5748-9. Williston. FGS V-5823 (Holman, 1959). Eichelberger Cave A. UF 5302.

In addition to those reported by Gilmore (1938) and Brattstrom (1953a), the following are reported from the additional Pleistocene and/or Recent localities: Itchtuckanee Springs I. UF 5204, 5206, 5208, 5229, 5302, 5274, Haile I, B. UF 5104.

Figure 27 illustrates the ontogenetic change in the ratio zw/cw. Figure 28 illustrates a typical mid-precaudal vertebra of this species.

Elaphe Dumeril and Bibron

Description.—Vertebrae of colubrid type, with well developed hypapophyses anteriorly, centrum triangular, moderate in length, slightly depressed, provided with a well developed haemal keel in the middle and posterior vertebrae. This keel is usually slightly expanded posteriorly, with subcentral ridges extending from the diapophyses to the condylus. The paradiapophyses are below, usually behind the prezygapophyses, with two articular facets, and the parapophysial process is not projected greatly

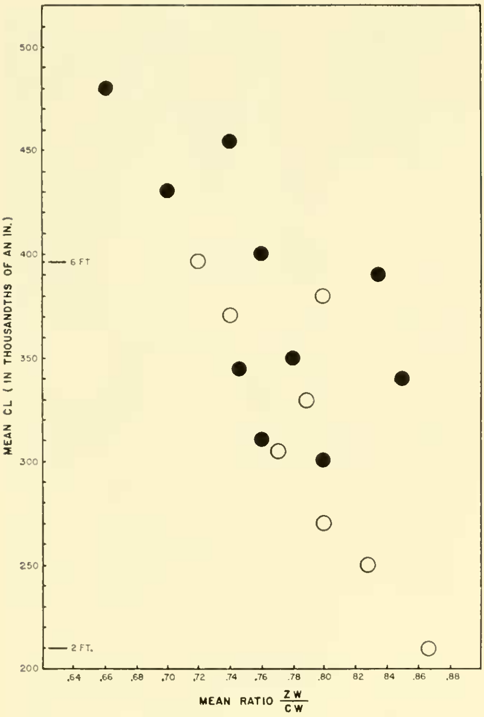

Figure 27. The mean ratio zw/cw plotted against cl to illustrate ontogenetic changes in this ratio in *Drymarchon corais*. Circles = modern specimens, dots = fossil specimens.

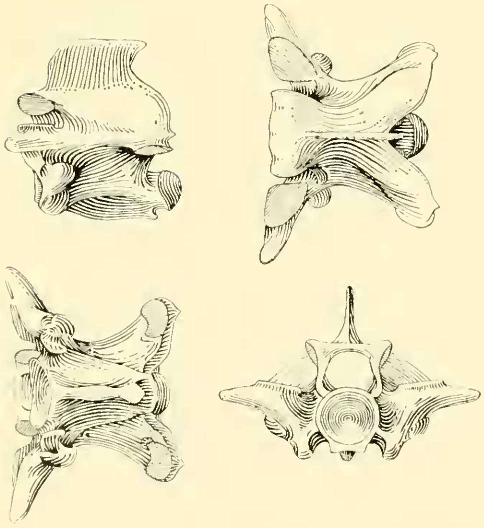

Figure 28. A precaudal vertebra of *Drymarchon corais* (UF 5079) Arredondo I A, Pleistocene (Illinoian ?).

below the centrum. The interzygapophysial ridges are evident. The prezygapophysial articular facets are oval to obovate, with the accessory processes directed downward to laterally from the front, laterally from the top; condylus directed more posteriorly than dorsally. The cotyle is slightly horizontally oval in young specimens, or in the anterior vertebrae of some adults, changing to round, or even vertically oval in the posterior thoracic vertebrae of large specimens. Neural arch moderate in height, not greatly flattened from behind. The zygosphene is about as wide as the narrowest part of the neural arch, being convex, straight or rarely concave from above, with or without a median notch, convex to straight from the front. Epizygapophysial spines usually absent, but sometimes feebly developed in large specimens. Neural spine almost always as high as long, lower in young specimens and in large adults.

The vertebrae of the genus *Elaphe* are sometimes difficult to separate from at least some species of *Lampropeltis, Arizona,* and *Pituophis*, among North American snakes. From the former the vertebrae of *Elaphe* may be separated by the presence of subcentral ridges which are straight, not bent from below as they are in most species of *Lampropeltis* (Brattstrom, 1955a). Furthermore, these ridges are more strongly developed in *Lampropeltis*. From *Pituophis, Elaphe* is most easily distinguished by the higher neural spine of the former, the more strongly developed epizygapophysial spine of the former, and the shape of the zygosphene, which is practically always concave from above in *Pituophis*, and rarely so in *Elaphe*. However, small specimens of *Pituophis* approach *Elaphe* in all of these characters. Exceptionally large examples of *Elaphe* may approach the vertebral structure more characteristic of *Pituophis*. Identification of individual vertebrae of *Elaphe, Lampropeltis* and *Pituophis* is frequently a specific rather than a generic identification. The reason is that the formulation of a series of characters for a generic definition is difficult.

At least representative portions of the vertebral column of the following species of *Elaphe* have been examined: *Elaphe obsoleta* (12, including the subspecies *lindheimeri, quadrivittata, obsoleta,* and *spiloides*), *E. subocularis* (1), *E. guttata* (6, including the subspecies *guttata* and *laeta*), *E. climacophora* (1), *E. dione* (1), *E. situla* (1), *E. vulpina gloydi* (1), and *E. taeniurus* (1).

E. situla apparently is separable from the species listed above on the basis of the hypapophysial keel, which is more expanded just anterior to the condylus. *E. dione* apparently is characterized by its extremely narrow zygosphene (cl/zw 1.81, varying from 1.09-1.50 in all of the other species), its low neural spine (at least two times longer than high, being higher in other species), which overhangs anteriorly (usually straight in other species). *E. vulpina* apparently is distinguished by possessing a longer centrum in the mid-dorsal vertebrae than in any of the remaining species (cl/naw = 1.09-1.18, and from 0.86-1.11 in the other species; cl/zw = 1.34-1.50, 1.09-1.33 in the other species). *E. taeniurus* and *E. climacophora* are similar to *E. obsoleta* and *E. guttata* as regards their middle dorsal vertebrae. *E. climacophora*, on the basis of one available specimen, may be separated by the ratio of the shortest length of the neural spine (nls), which is practically equal to the width of the zygosphene (zw). In the remaining species it is much less, regardless what part of the column is being considered. *E. taeniurus*, on the other hand, is similar to the two American species examined. No vertebral character was found which will consistently separate it from them. The fossil *Elaphe* from Florida clearly represents one or more of these three species. The remaining Pleistocene genera do not suggest the presence of any species now restricted to the Old World, and there is no reason to suppose that the condition is any different in *Elaphe*.

E. obsoleta and *E. guttata* may be separated readily on the basis of the relative height and width of the neural spine. However, there is considerable overlap in the ratios when they are taken by themselves. These ratios change with growth, and if the ratios are plotted against centrum length, the species are, for the most part, separable (fig. 29).

The fossil vertebrae of *Elaphe* fall along one curve or the other, and the vast majority of the specimens thus may be identified with some degree of certainty. The one available specimen of *E. taeniurus* has a different ratio than *E. obsoleta* or *E. guttata*, falling between them. However, since only one specimen is available, and since some variation in this character does exist (at least ontogenetically) the value of this difference as a diagnostic character is questionable. However, the character is constant in any individual specimen of *Elaphe*, disregarding the variation in the anterior portion of the column, where the vertebrae possess well developed hypapophyses. This relative constancy provides a character of considerable merit in distinguishing at least the two American species considered here.

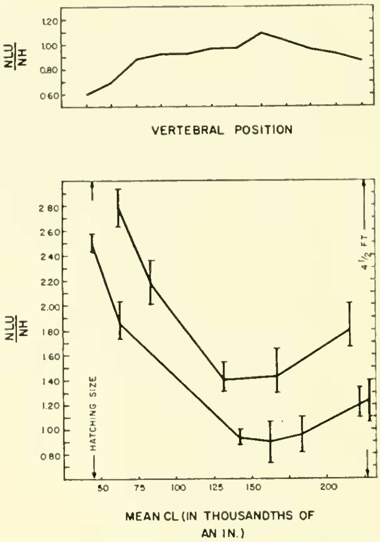

Figure 29. Upper: Intracolumnar variation in the ratio nlu/nh in one Recent, average-sized specimen of *Elaphe obsoleta*. The distance between marks along the horizontal axis is equal to 10 vertebrae. The first two vertebrae on the left are provided with hypapophyses. Lower: The same ratio plotted against mean cl in Recent specimens of *E. obsoleta* and *E. guttata*.

Of considerable interest and importance is a re-evaluation of the Pliocene genus, *Palaeoelaphe* Gilmore (1938: 64). The generic characters, according to Gilmore, concern its larger size, more robust hypapophyses with dilated distal ends which are truncate, and the flattened haemal keel. The latter occurs in almost all middle and posterior vertebrae of larger specimens of *E. obsoleta*. The anterior vertebrae of *E. obsoleta* have hypapophyses which are robust, as well as truncated. They are more elongate, and not as obviously truncated, in *E. guttata*. The shallow notch in the zygosphene of the type vertebra of *Palaeoelaphe* suggests *E. obsoleta*, but is sometimes found in large specimens of *E. guttata*. *Elaphe obsoleta* attains a much larger size than *guttata*. Thus, the majority of the characters of *Palaeoelaphe* fall closer to *obsoleta* than to *guttata*. The shape of the hypapophyses seems to be the most diagnostic character. This structure varies considerably within the genus, sometimes being remarkably adapted for specific feeding habits (Gans and Oshima, 1952; Gans, 1952). There is little evidence to indicate that *Palaeoelaphe* deserves recognition as a distinct genus, and every reason to believe that it should be referred to the synonymy of *Elaphe*. Furthermore, *Elaphe* (*Palaeoelaphe*) *kansensis* is closest to *obsoleta*, and probably is ancestral to it.

Elaphe obsoleta Say

The generic description of the vertebrae suffices since the American species considered in this paper are similar. To separate this species from *E. guttata* reference should be made to Figure 29. A mid-precaudal vertebra of *Elaphe obsoleta* is illustrated in Figure 30. Table 15 compares some of the vertebral ratios of Pleistocene and Recent *Elaphe obsoleta* and *E. guttata*.

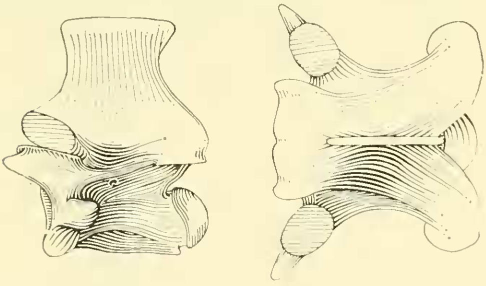

Figure 30. A precaudal vertebra of *Elaphe obsoleta* (UF 5177) Reddick I B, Pleistocene (Illinoian ?).

Elaphe obsoleta was collected from the following *Pleistocene* localities in Florida: Haile VII, A. UF 5177, 6270, 5173. Reddick I, B. UF 6444, 5605, 5177, 5049, 5567, 5694, 6264. Kanapaha I, A. UF 6118.

This species has been collected also from the Pleistocene and or Recent locality of Itchtuckanee Springs, Locality A. (UF 5260). Brattstrom (1953a) reported it from Seminole Field (AMNH 7176).

Elaphe guttata Linnaeus

Figure 29 illustrates the method by which the vertebrae of this species are separated from those of *E. obsoleta*. Table 15 compares some of the vertebral ratios of Pleistocene and Recent *E. obsoleta* and *E. guttata*. Figure 31 illustrates a middle precaudal vertebra of *E. guttata*. Because of the degree of ontogenetic change in vertebral proportions and its importance as a character used to distinguish between this species and *E. obsoleta*, the ontogenetic changes in vertebral form of a middle precaudal vertebra are shown in Figure 32.

Elaphe guttata was collected from the following Pleistocene localities in Florida: Reddick I, B. UF 4309, (3)—10, 6290 (3), 6116, 6086, 6052, 6288 (2), 6091, 9878, 9890-1, 5480, 4310, 5690, 5808, 6366, 6462, 6163. Arredondo I, E. UF 6024-6. Arredondo II, A. UF 2077. Mefford Cave I, A. UF 2557. Eichelberger Cave B. UF 6161. Haile I, A. UF 5480, 5037. Haile II, B. UF 6031, 5041, 6030, 5683-4, 5633-4, 5679-80, 5681. Payne's Prairie B. UF 5754. Winter Beach. UF 5833, 5839.

Holman (1958, 1959) reported *Elaphe* sp. from both Sabertooth Cave and Williston.

In addition, the species is known from Itchtuckanee Springs A, a locality considered Pleistocene and or Recent in age (UF 5386, 5405, 5403, 5398).

TABLE 15.
A comparison of certain vertebral ratios in Recent and Pleistocene specimens of Elaphe obsoleta and Elaphe guttata

	E. obsoleta		*E. guttata*	
Ratios	Pleistocene (N=15)	Recent (N=52)	Pleistocene (N=46)	Recent (N=50)
cl/naw	0.93-1.03	0.86-1.11	0.95-1.01	0.96-1.04
pr-pr/po-pr	1.28-1.31	1.23-1.36	1.25-1.27	1.21-1.29
cw/zw	1.10-1.17	1.07-1.25	1.13-1.20	1.08-1.23
cl/zw	1.12-1.16	1.08-1.33	1.09-1.20	1.03-1.36
nlu/nls	1.11-1.14	1.08-1.18	1.14-1.21	1.10-1.23
nlu/nh	1.01-1.05	0.94-1.17	0.92-1.16	0.89-1.21
cl/nlu	1.25-1.31	1.18-1.48	1.20-1.26	1.16-1.31

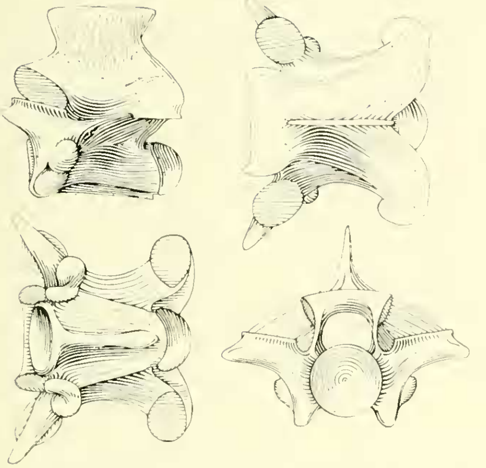

Figure 31. A precaudal vertebra of *Elaphe guttata* (UF 5684) Reddick I B, Pleistocene (Illinoian ?).

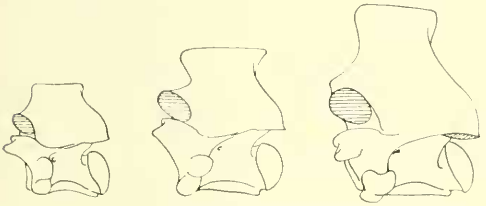

Figure 32. Ontogenetic change in the shape of the precaudal vertebrae of *Elaphe guttata*. Left: hatchling. Middle: specimen 2½ feet long. Right: specimen 4½ feet long.

Based solely on the amount of material available from the Pleistocene deposits of Florida, *E. guttata* may have been more widely distributed and more common than *E. obsoleta*. However, paleoecological conditions in the vicinity of the deposits may have been such to favor habitation by *guttata* rather than *obsoleta*.

Pituophis Holbrook

Description.—Centrum moderate in length, subtriangular from below, with strong subcentral ridges, extending from the posterior edge of the diapophyses posteriorly to the condylus. The haemal keel is gladiate to sub-spatulate in shape, extending from the lower lip of the cotyle to near the condylus. Condylus on a short neck, facing posteriorly more than dorsally. Cotyle rounded, but sometimes vertically oval in vertebrae at the posterior part of the body of large specimens. Paradiapophysial facets double, the diapophysial facet more or less above the lower parapophysial facet. The former is also larger and more convex. The neural arch is moderate to high, usually without epizygapophysial spines in smaller specimens, to moderately developed in larger individuals. Zygosphene thin, concave from above, convex from the front, sometimes with a slight median notch. Neural spine as long, or higher than long, sometimes slightly overhanging anteriorly, but usually rather straight, overhanging posteriorly. Prezygapophyses well developed, the articular facets oval. The accessory processes are acutely pointed, moderately long, directed anteriorly from above, laterally to slightly upwards from the front. The postzygapophyses are oval to obovate in shape.

The genus is most easily confused with *Elaphe*. From that genus it can be separated by the concave zygosphene from above (only rarely so in *Elaphe*), the somewhat better developed epizygapophysial spines, and the neural spine, which is usually much higher in *Pituophis*.

The following specimens have been used for comparative purposes: *Pituophis m. melanoleucus* (2), *P. m. mugatus* (4), *P. c. catenifer* (1), *P. c. annectens* (1), *P. c. deserticola* (1) and *P. c. sayi* (3).

On the basis of the available comparative material, *P. catenifer* possesses lower neural spines than does *P. melanoleucus* (nlu nh: *catenifer* 1.14-1.22, *melanoleucus* 0.90-1.16). However, the specimens of *catenifer* available for study were smaller than those of *melanoleucus,* and the character may be associated with growth and or age. The fossil vertebrae from Florida all possess the high neural spines found in the modern skeletons of *melanoleucus*, and they thus are referred to this species.

Pituophis melanoleucus Daudin

The apparent vertebral differences between *catenifer* and *melanoleucus* have been pointed out above. Figure 33 illustrates a typical middle precaudal vertebra of this species. Table 16 compares the vertebral ratios of modern specimens of *P. melanoleucus* and Pleistocene specimens referred to this species.

Pituophis melanoleucus vertebrae are known from the following Pleistocene localities in Florida: Reddick I, B. UF 5000-1, 5003-8, 5102, 6143, 5812. Kanapaha I. UF 6017. Williston. FGS V-5805 (Holman,

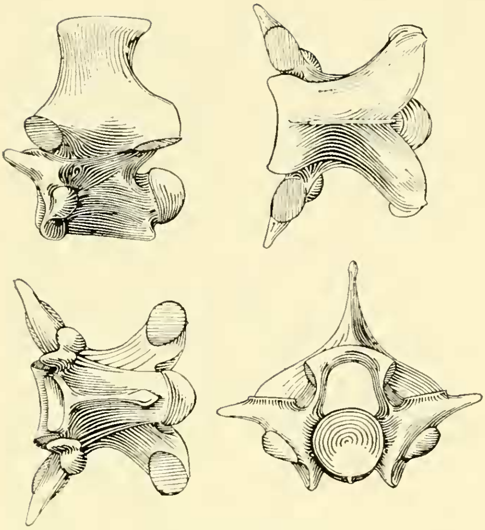

Figure 33. A precaudal vertebra of *Pituophis melanoleucus* (UF 5002) Reddick I B, Pleistocene (Illinoian ?).

1959). Eichelberger Cave B. UF 6180.

In addition, the species is known also from Itchtuckanee Springs, I. (UF 5275-8, 5231), a locality classed as Pleistocene and/or Recent. Brattstrom (1935a) reported this species from Vero Beach, Stratum 3, and Seminole Field.

Lampropeltis Fitzinger

Description.—Centrum moderate in length, the anterior series possessing well-developed hypapophyses, which are reduced in the middle and posterior series to a haemal keel. However, within the genus there is considerable variation in the development of the keel. It is low and somewhat broad in some forms, especially the posterior series, whereas it is high and narrow in young specimens, or in *L. doliata, L. multicincta, L. zonata* and *L. polyzona,* and especially small individuals of these species.

TABLE 16.
A comparison of some vertebral ratios of Recent and Pleistocene specimens of Pituophis melanoleucus

Ratios	Pleistocene (N=38)	Recent (N=45)
cl/naw	0.94-1.07	1.05-1.18
ctw/cth	1.02-1.11	1.00-1.17
pr-pr/pr-po	1.05-1.32	1.13-1.31
zw/naw	0.72-0.89	0.83-0.98
cl/zw	1.11-1.31	1.10-1.28
nlu/nh	0.90-1.12	0.90-1.16
nlu/nls	1.06-1.14	1.10-1.24

The subcentral ridges extend from the posterior portion of the diapophyses posteriorly to near the condylus. The haemal keel is usually gladiate-shaped, with an acute posterior tip. The cotyle is round. The condylus is on a short neck, directed more posteriorly than upwards. The neural arch is strongly depressed in all but the anterior vertebrae. Epizygapophysial spines are absent. The zygosphene is thin, crenate, straight or convex from above, convex from the front. The articular facets are obovate to oval in outline. The neural spine is somewhat variable in shape, being very low and long in the *doliata* group, and higher in *calligaster* and *getulus.* It is always overhanging posteriorly, and either straight or overhanging anteriorly.

Comparative material examined includes the following skeletons: *Lampropeltis z. zonata* (1), *L. z. multicincta* (1), *L. polyzona* (1), *L. g. getulus* (3), *L. g. holbrooki* (1), *L. g. splendidus* (1), *L. g. californiae* (1), *L. c. rhombomaculata* (1), *L. c. calligaster* (1), *L. d. doliata* (3), *L. d. syspila* (1) and *L. d. triangulum* (3).

On the basis of the comparative material apparently within the genus *Lampropeltis* there are at least two groups which may be distinguished on vertebral characters. These are, (1) the somewhat smaller species, composed of *zonata, polyzona.* and *doliata* and, (2) the larger forms, composed of *getulus* and *calligaster.*

Other than size (a poor character), these two groups can be distinguished on the basis of the relative height of the neural spine (Table 17). Group 1 may be confused with *Rhadinea,* from which it may be separated by the ratio cl/naw (0.94-1.17 in Group 1 of *Lampropeltis,* 1.42-1.64 in *Rhadinea*). Furthermore, the haemal keel of *Rhadinea* usually is more flattened than it is in *Lampropeltis,* with the exception of *L. d. triangulum.* Some species of *Liophis* and *Leimadophis* have vertebrae similar to those of *Lampropeltis.* Usually they can be separated on the basis of the development of the subcentral ridges, which are weakly developed in *Liophis* and *Leimadophis,* stronger in *Lampropeltis.*

Group 2 is confused easily with *Rhinocheilus* and *Cemophora.* From the former it may be distinguished in that it lacks the

TABLE 17.
Comparison of certain vertebral ratios in Recent skeletons of Lampropeltis

	cl/naw	ctw/cth	pr-pr/po-pr	zw/naw	cl/zw	nlu/nh
calligaster (N=22)	1.00-1.18	1.00-1.08	1.23-1.33	0.95-0.98	1.20-1.30	1.04-1.18
getulus (N=55)	0.85-1.11	0.92-1.10	1.10-1.45	0.67-0.95	1.05-1.50	1.12-1.53
zonata (N=18)	1.00-1.03	1.01-1.04	1.19-1.24	0.94-0.98	1.01-1.06	4.00-4.10
doliata (N=27)	1.04-1.17	1.02-1.09	1.05-1.16	0.85-0.97	1.07-1.38	2.70-4.28
polyzona (N=21)	0.92-1.00	1.05-1.12	1.39-1.54	0.95-0.99	0.95-1.02	2.30-3.20

much thicker neural spine of *Rhinocheilus*. In addition, the upper edge of the spine in *Lampropeltis* is sharp, not flattened as in that genus. From *Cemophora, Lampropeltis* may be separated by its more depressed neural arch and in having a much greater overhang on both the anterior and posterior edges of the neural spine. From *Elaphe, Pituophis, Salvadora,* and *Arizona* it may be separated by its more depressed neural arch and, in general, the better developed subcentral ridges. *Stilosoma* is different in a number of characters; a much shorter neural spine, paradiapophysial articular facets not well separated, a strongly concave zygosphene when seen from above, a neural arch which is much less depressed, and an oval cotyle. On the basis of vertebral form only it is difficult to see how *Stilosoma* can be related to *Lampropeltis*. If any relationship exists between the two genera it will certainly be remote. In fact, among North American colubrid snakes, *Stilosoma* appears unique in vertebral form.

Brattstrom (1955a) illustrated the vertebrae of a number of species of *Lampropeltis*, describing the subcentral ridges and pointing out differences between the various species in this character. After examining the comparative material available to me, I find a somewhat less clear demarcation between the various species than was indicated by Brattstrom. However, there is a general tendency for these ridges to be bent in *getulus*, whereas they are convex, concave, or straight in the other species examined. Both inter- and intracolumnar variation is exhibited in this character. However, if only middle precaudal elements are compared, their utility in a diagnosis is warranted. All the remaining characters given by Brattstrom as diagnostic seem to be valid.

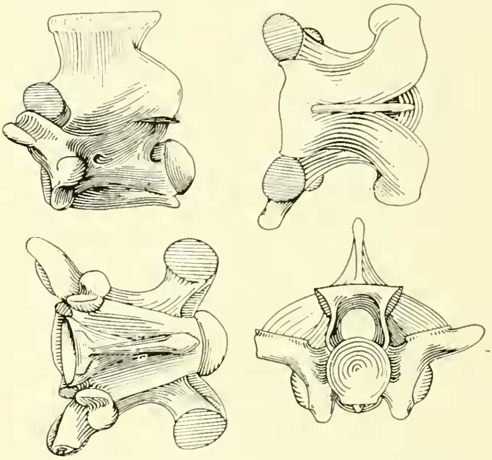

Figure 34. A precaudal vertebra of *Lampropeltis getulus* (UF 5153) Haile VII A, Late Pleistocene (Illinoian ?).

Lampropeltis was reported from the Pliocene of North America (Brattstrom, 1953a, b, c, 1954b). *Lampropeltis doliata* and *L. getulus* were reported from Seminole Field. The latter has, in addition, been reported from Melbourne (Brattstrom, 1953c). These localities are considered Pleistocene and/or Recent. He also reported *L. getulus* from the Pleistocene locality of Allen Cave (AMNH 6772). In addition, the following localities should be added: *Pleistocene:* Reddick I, B. UF 6296. Arredondo I, A. UF 5924, many vertebrae from one individual. Haile VII, A. UF 6308, 6325, 5173, 6270, 5153, 6193, 6396. Haile I, A. UF 5472. *Pleistocene and/or Recent:* Itchtuckanee Springs, A. UF 5448, 5386.

A typical middle precaudal vertebra is illustrated in Figure 34.

Stilosoma Brown

One mid-precaudal vertebra from the Pliocene locality of Haile VI, A, is not only unique, but interesting because it provides some information as to the length of time that *Stilosoma,* an endemic Florida genus, has been present in the peninsula. The basic structure of the single element is similar to that in the modern species, *S. extenuatum,* and the vertebra is provisionally referred to that genus. Additional material should be helpful in determining its exact generic status. *Stilosoma* has never before been reported in the fossil record. The new form may be known as:

STILOSOMA **VETUSTUM**, *sp. nov.*

Diagnosis.—A Pliocene colubrid snake most closely resembling the modern genus *Stilosoma,* but differing from the living species, *extenuatum,* in the narrower and somewhat more ridge-like haemal keel. *Stilosoma* is distinguished from all other modern or fossil New World colubrids I have seen in possessing a very short, wide vertebra, by the small prezygapophyses, by the low, but not excessively long neural spine and a reduction of the division between the two articular surfaces of the paradiapophyses.

Holotype.—UF 6467, a fairly complete vertebra, collected June, 1954, by Walter Auffenberg.

Type Locality and Horizon.—Haile VI, A, near Haile, Alachua County, Florida, Middle Pliocene, Hemphilian, Alachua fm.

Description of the Type.—One vertebra which is similar in size and structure to those found in *Stilosoma extenuatum,* except as mentioned above. The upper portion of the neural spine is broken off, as are the accessory processes on both sides. The centrum is short and wide, triangular from below, possessing moderately strong subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, directed posteriorly. Paradiapophyses well developed, but the separation between the two surfaces not as distinct as in most colubrids. The parapophysial surface is much smaller than the diapophysial one. Parapophysial process not projected downwards or anteriorly beyond the ventral margin of the cotyle. Cotyle somewhat oval horizontally, the edge broken on the right side. Neural arch wide, depressed, without epizygapophysial spines. Neural spine presumably low on the basis of the thin broken edge. Prezygapophysial surfaces oval, broken on the right side, small as in *Stilosoma extenuatum.* Zygosphene worn in the type, but convex from above and from the front on the basis of the remainder of the structure, thin dorso-ventrally. Neural canal moderately large, somewhat oval from the front. Haemel keel broadly gladiate, but not overly flattened.

The type vertebra is compared with a vertebra of a recent specimen of *Stilosoma extenuatum* in Figure 35.

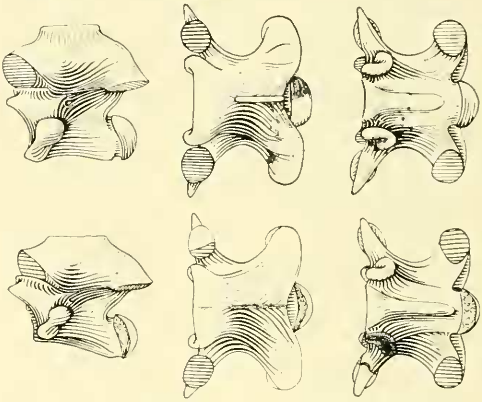

Figure 35. Upper: A precaudal vertebra of *Stilosoma extenuatum.* Lower: The type vertebra (UF 6467) of *Stilosoma vetustum,* sp. nov., Haile VI A, Alachua Co., Florida, Alachua fm. (restricted), Middle Pliocene (Hemphillian).

(?) *Stilosoma extenuatum* Brown

A single vertebra (UF 2076) from the Pleistocene locality of Arredondo II, A may represent the short-tailed snake, *S. extenuatum.* However, the element is somewhat fragmental, and even the generic assignment is tentative until more material becomes available.

The genus *Stilosoma* is usually considered close to *Lampropeltis.* Only one Recent vertebral column is at present available for study. This specimen is rather small, and at least some ontogenetic change is expected in larger individuals. However, a comparison of the vertebrae of this specimen with those from a number of modern species of *Lampropeltis* indicates many differences. The ontogenetic change in the vertebral form of *S. extenuatum* should not be so great that these differences would be nullified. This view is supported by the fossil vertebra from Haile VI, which apparently represents a snake about two feet long (or about the size of an average specimen of *S. extenuatum*), yet it is similar to that of the smaller comparative Recent specimen.

The relict distribution of the genus, as well as its external characteristics, seem to indicate that it has been separated from its closest relatives for a long time. This view is certainly substantiated by the vertebral form of this genus. It is, in fact, so different from all of the available skeletons of New World colubrids that one is tempted to look for possible relatives among the Old World genera; a search that has, as yet, been unsuccessful.

PSEUDOCEMOPHORA, *gen. nov.*

Diagnosis.—A Miocene colubrid, closest to *Lampropeltis* and *Cemophora* in vertebral characters, but differing from these in the following characters: from the former in the shape of the haemal keel when seen from the side, in that it does not extend anteriorly to the lower lip of the cotyle. From *Cemophora* it differs chiefly in the longer vertebrae, the lower neural spine, the subcentral ridges originating lower on the paradiapophyses. In the same deposit it is most easily confused with *Ogmophis*, but separated on the basis of its longer centrum and the better developed diapophysial articular facets.

Genotype.—*Pseudocemophora antiqua,* sp. nov.

PSEUDOCEMOPHORA ANTIQUA, *sp. nov.*

Diagnosis.—Sole known species of the genus.

Holotype.—UF 6458, a fairly complete precaudal vertebra, collected March, 1954, by Walter Auffenberg (Fig. 36).

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Lower Miocene (Arikareean), Hawthorne fm.

Referred Material.—UF 5744; four somewhat more fragmentary vertebrae, collected at the same time from the same locality.

Type Description.—A colubrid vertebra with a relatively long centrum, which is provided with a sharp to truncated, haemal keel, extending from the cotyle to near the condylus, with a slight depression in the keel at approximately one third of its length. The subcentral ridges are well developed, extending from the diapophyses to the condylus. There are deep grooves between these ridges and the haemal keel. The paradiapophyses are well developed, with the parapophysial part possessing an articular facet which is well separated from the diapophysial one. The parapophysis is projected downwards and anteriorly to the ventral edge of the centrum. The neural arch is moderately low, long, and without epizygapophysial spines. The neural spine is long, low, overhanging posteriorly, straight anteriorly. Cotyle nearly round, but not distinctly oval. The condylus is on a short neck, projected backwards and slightly upwards. The zygosphene is crenate from above, convex from the front. Prezygapophysial articular surfaces probably obovate, but broken. The accessory processes are broken in the type, but in some of the referred specimens they are long, acute to acuminate, directed slightly anteriorly from above, laterally from the front. Measurements of vertebrae are given in Table 18.

Of particular interest is the relationship of this extinct genus with the modern forms. Along with *Paraoxybelis* (gen. nov.) it shares the distinction of being the earliest known colubrid from North America. Its relationships are apparently with, or close to *Cemophora, Rhinocheilus,* or *Lampropeltis,* espe-

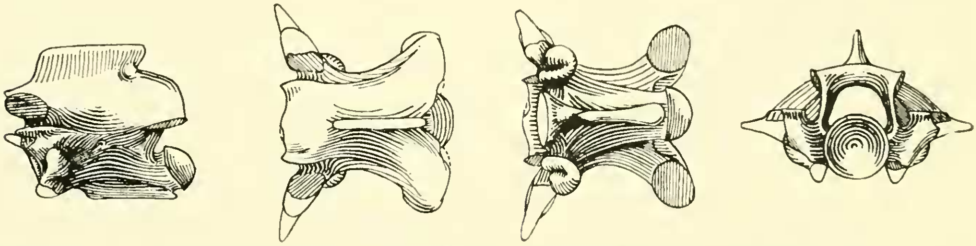

Figure 36. The type vertebra (UF 5744) of *Pseudocemophora antiqua,* gen. nov., et sp., Thomas Farm, Gilchrist County, Hawthorne fm., Lower Miocene (Arikareean).

Table 18.
Important measurements (in mm) and ratios of the available vertebrae (5) of Pseudocemophora antiqua

cl	2.52-3.15
naw	1.80-2.08
col	0.43-0.91
naw/cl	0.64-0.75
nlu/nh	2.47
zw	1.65-1.70
nh	0.61-0.81
ctw	0.94-1.07
ctw/cth	1.04-1.11
cl/nh	1.90-2.20
nlu	2.01
pr-pr	3.63
cth	0.86-1.09
cl/zw	1.47-1.54

cially the *doliata* group. Of these three genera, the available fossil vertebrae are closest to *Cemophora.*

In addition to the vertebrae, one small palatine (UF 6144, Fig. 37) is referred to this genus and species. In size, shape, and the number of teeth it seems close to *Lampropeltis* and *Cemophora.*

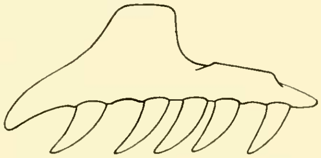

Figure 37. A palatine (UF 6144) from the Lower Miocene Thomas Farm locality, tentatively referred to *Pseudocemophora antiqua.*

The somewhat intermediate nature of the vertebrae and the palatine provisionally placed with them, is not surprising in view of the age of the fossils. *Lampropeltis* is frequently placed close to *Cemophora* by workers studying the Recent forms. However, too little is known of the extinct snake fauna of North America beyond the Pleistocene to draw any conclusions of evolutionary significance from this isolated find of elements apparently representing this group. It is of interest to know that such a form existed in the Lower Miocene, but the more important question of whether or not it is ancestral to either *Lampropeltis* or *Cemophora,* or both, is unknown at the present time.

Tantilla Baird and Girard

Description.—Middle precaudal vertebrae with a long centrum, with the subcentral ridges either weakly developed, or sometimes even absent. The haemal keel is narrow, keel-like, to gladiate in shape; or in some species even flattened, broad, oblanceolate, or cunate. There are two articulating surfaces on the paradiapophyses. The parapophysial process is only slightly projecting. The condyle is directed backwards more than upwards. The cotyle is rounded to very slightly oval. Neural arch long, low, depressed, without epizygapophysial spines. Neural spine long, low, with straight anterior and posterior edges. Zygosphene crenate to convex from above, convex from the front. Prezygapophysial facets oval to obovate. Accessory processes well developed, acuminate to acute, directed slightly anteriorly from above, and slightly downward from the front.

Comparative material includes the following: *Tantilla coronata* (3), *T. eiseni* (2), *T. nigriceps* (1) and *T. melanocephalus* (1). All of these species show the closest agreement in structure and vertebral ratios, and I find them impossible to tell apart. Remains of this genus from the Pleistocene of Florida are tentatively referred to *coronata,* which occurs in the peninsula at the present time. The genus has not been reported as a fossil previously.

Tantilla coronata Baird and Girard

This species is known from two localities in the State, Reddick I, B, from which a number of vertebrae are available (UF 6081, CNHM, PR. 375) and Arredondo I, A (UF 5921). Both of these localities are Middle or Late Pleistocene (Illinoian?).

Table 19 compares the vertebral ratios of Recent and Pleistocene vertebrae of this species. Figure 38 illustrates a middle precaudal vertebra.

PARAOXYBELIS, *gen. nov.*

Diagnosis.—A miocene colubrid snake which differs markedly from other known Miocene snakes in possessing a much longer centrum, a spatulate-shaped, flattened haemal keel, and very large prezygapophysial articular surfaces. In centrum length this form is approached only by *Oxybelis, Leptophis,* and *Uromacer* among New World colubrid snakes.

From *Oxybelis* and *Uromacer* it is distinguished clearly in not possessing the greatly overhanging anterior edge of the neural spine as is found in these two genera. From

Table 19.
A comparison of certain vertebral ratios in Pleistocene and modern specimens of Tantilla coronata

Ratios	Recent (N=40)	Pleistocene (N=33)
cl/naw	1.61-1.86	1.57-1.84
naw/zw	0.96-1.00	0.98-1.00
nlu/nh	3.21-7.80	3.68-7.73
pr-po/pr-pr	0.97-1.03	0.98-1.01
ctw/cth	1.00-1.06	0.98-1.03

Leptophis it differs chiefly in its higher neural spine (nlu/nh: *Paraoxybelis* 3.24; *Leptophis* 2.48-2.59). In addition, it differs from these three genera in its larger prezygapophysial articular facets and the spatulate-shaped haemal keel, which is broadly gladiate in the three modern genera.

Genotype.—*Paraoxybelis floridanus,* sp. nov.

PARAOXYBELIS **FLORIDANUS**, *sp. nov.*

Diagnosis.—The sole known species of the genus. The generic diagnosis is given above.

Holotype.—UF 5134, a fragmentary precaudal vertebra, collected by Walter Auffenberg, March, 1954.

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Hawthorne fm., Lower Miocene (Arikareean).

Type Description.—Vertebra typically colubrid. Centrum long, slightly depressed. Haemal keel flattened, extending from the lower lip of the cotyle to near the condylus, spatulate-shaped. Anteriorly the keel expands rapidly near the cotyle. Centrum flattened on either side of the keel. Subcentral ridges straight, well developed, extending from the diapophyses posteriorly to the condylus. The condylus is on a neck of moderate length, directed slightly obliquely. Cotyle round, narrower than the zygosphene. Paradiapophyses below, but set just under the base of the prezygapophyses, the two articular surfaces facing outward and downward. The diapophysial articular surface is somewhat oval, while the parapophysial one is more flattened, and pointing downward and slightly to the front, extending moderately below the level of the cotyle. Neural arch somewhat depressed, but not greatly. Epizygapophysial spines apparently missing. Neural spine long, low, not overhanging anteriorly or posteriorly. Zygosphene thin dorso-ventrally, with the facets approximately 45 degrees to the vertical, slightly crenate from above, convex from the front. Prezygapophysial articular facets oval, large, with very small accessory processes. Interzygapophysial ridges well developed. Neural canal nearly as wide as the zygosphene.

Two other vertebrae are tentatively assigned to this species. These are; UF 6007a, a well preserved caudal vertebra, and UF 6007b, a fragmentary precaudal vertebra, composed of only the centrum. In as many details as can be compared these specimens are similar to the type. The caudal vertebra has a proportionately higher neural spine in which both the anterior and posterior upper margins are somewhat overhanging. The smaller prezygapophysial articular facets of this vertebra, when compared with the type, are to be expected in the caudal region.

The specimen represented by a centrum only is logically placed with *P. floridanus,* on the basis of the ratio cl/naw if on no other. As in the type, the centrum is long and narrow and the haemal keel is flattened and spatulate.

All of the available fossil vertebrae suggest an attenuate species of snake. When these fossils are compared with *Coluber* and *Masticophis* a considerable number of differences are found, with the exception of a general agreement in the shape of the haemal keel. Thus, the neural spine is different in shape; and the centrum is considerably

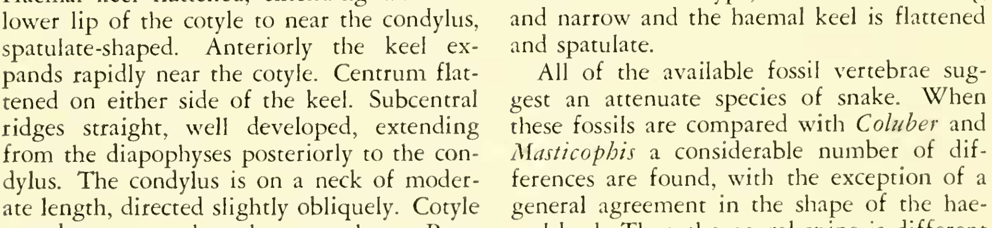

Figure 38. A precaudal vertebra of *Tantilla* cf. *coronata* (UF 6081) Reddick I B, Pleistocene (Illinoian ?).

longer (cl/naw: *Coluber* 1.40-1.51; *Masticophis* 1.19-1.64; *Paraoxybelis* 1.86-1.99). On the other hand, the spatulate haemal keel is approached in *Coluber* and *Masticophis*, particularly the former.

The centrum length of *Paraoxybelis* is approached by *Leptophis* (cl/naw = 1.73-1.92), *Oxybelis* (cl/naw = 1.56-2.11) and even exceeded by *Uromacer* (cl/naw = 1.97-2.03). However, all of these genera differ in a number of regards, as has been pointed out above.

Among the Old World colubrid snakes, the vertebrae of *Chlorophis* are slightly shorter (cl/naw = 1.57-1.66), and those of *Dryophis* even longer (cl/naw = 2.20-2.28). In addition to the large prezygapophysial articular facets, the shape of the haemal keel, etc., clearly separates *Paraoxybelis* from these genera.

Of all the vertebral ratios which can be compared with those of modern genera, the closest agreement is found in the New World genus *Oxybelis*. However, the spatulate-shaped haemal keel and the large prezygapophysial articular facets are not found in *Oxybelis*. Thus, the relationships of the Miocene snake remain obscure, though it may be closer to *Oxybelis* than to any other Recent New World genus. This possible relationship is interesting in that another new genus of colubrid snake from the Upper Miocene of North America (Auffenberg, 1958) also may be closely related to a Central American snake, *Conophis*.

Figure 39 illustrates the available vertebrae of *Paraoxybelis floridanus*, while Table 20 gives the available vertebral ratios of this species.

TABLE 20.
The available vertebral ratios of Paraoxybelis floridanus (N = 2)

cl/naw	1.86-1.99
zw/naw	0.84
cl/nlu	1.47
cl/col	4.00-5.81
nlu/nls	1.19
naw/nah	2.20
cl/zw	1.64-2.20
nlu/nh	3.25
pr-po/col	1.18

2. *Subfamily Natricinae*

Description.—Colubrid vertebrae which possess well developed hypapophyses on all of the vertebrae. Epizygapophysial spines are usually present. The vertebrae are usually long, with well developed, acuminate to acute accessory processes, which are directed mainly laterally from above and from the front. The parapophyses are nearly always projected downwards and anteriorly so that they extend beyond the lower level of the centrum and the margin of the cotyle.

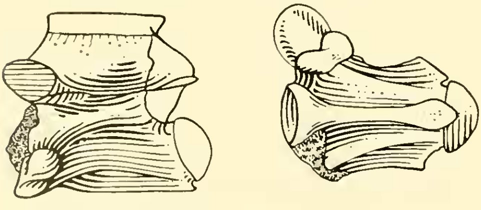

Figure 39. Left: Type vertebra (UF 5143) of *Paraoxybelis floridanus*, gen. nov. et sp., Thomas Farm, Gilchrist County, Hawthorne fm., Lower Miocene (Arikareean). Right: (UF 6007), a fragmental vertebra from the same locality, and referred to the same species.

The problems in identifying vertebrae belonging to this subfamily are great. The main reason is simply that all snakes possess hypapophyses in at least the anterior part of the column. It is not always a simple matter to separate middle dorsal vertebrae of a natricine from anterior dorsals of a colubrine although in most cases this is possible. Furthermore, the various natricine genera possess vertebrae similar to one another, so in many cases certain genera and species can not be separated even after one is positive that the vertebrae belong to this subfamily. For the most part, anterior vertebrae are easy to recognize, largely on the basis of the ratio cl/naw. In anterior vertebrae the centrum is shorter in proportion to the width than in the middle or posterior series. A comparison of this ratio in the anterior portion of the column in the Colubrinae with the entire column in the Natricinae will usually indicate sufficient differences between the various portions of the column so that middle precaudal members may be recognized by this means alone. As pointed out previously, the middle dorsal vertebrae are, by far, the best vertebrae to use in identifying fossils.

Characters other than the ratio cl/naw may be useful in separating anterior and middle dorsal vertebrae. However, in many cases, the determination of middle dorsal vertebrae remains difficult at best, and here identifications are based more on the composition of the entire sample than on individual vertebrae. With the entire sample considered as a unit the middle precaudal elements become evident. In any case, the anterior vertebrae of colubrid snakes must be recognized as such before the middle precaudal vertebrae of the Natricinae can be compared.

Because of the considerable similarity between the vertebrae of various genera of this subfamily, the comparative material is listed below as a unit, rather than listed below each species as had been done in the Colubrinae. Skeletons of the following forms have been examined: *Seminatrix pygaea* (4), *Liodytes alleni* (8), *Haldea striatula* (3), *Haldea valerae* (1), *Storeria dekayi* (5, representing 3 subspecies), *Storeria occipitomaculata* (2, representing 2 subspecies), *Tropidoclonion lineatum* (2, representing 2 subspecies), *Thamnophis elegans hammondi* (1), *Thamnophis sirtalis* (6, representing 3 subspecies), *Thamnophis radix* (2, representing 2 subspecies), *Thamnophis sauritus* (6, representing 3 subspecies), *Thamnophis ordinoides* (1), *Thamnophis cyrtopsis* (1), *Thamnophis marciana* (1), *Thamnophis brachystoma* (1), *Natrix natrix* (2, representing 2 subspecies), *Natrix tesselatus* (1), *Natrix stolata* (1), *Natrix grahami* (1), *Natrix septemvittata* (4), *Natrix harteri* (2), *Natrix rigida* (1), *Natrix rhombifera* (2), *Natrix taxispilota* (6), *Natrix cyclopion* (6, representing 2 subspecies), *Natrix sipedon* (14, representing 6 subspecies), *Natrix erythrogastor* (2).

Various genera of snakes belonging to the family Colubridae possess hypapophyses besides those placed in the Natricinae. These include members of the Colubrinae, Xenoderminae, and Xenodontinae. The Xenoderminae are distinct and present no major problems in identification. On the other hand, certain colubrine and xenodontine genera are difficult to separate from the Natricinae on the basis of the middle precaudal vertebrae. In some of these genera the hypapophyses are found only on the posterior members of the column. These may be extremely difficult, if not impossible, to separate from natricines if only a few vertebrae are available. *Helicops* is such a form. Comparative material of this genus includes two species, *leopardinus* (2 specimens) and *caricaudae* (1 specimen).

Several colubrid genera possess a haemal keel which may become so well developed in individual species, or even specimens, that it must be considered a hypapophysis. Of the material I have examined, *Ninia* is an excellent example of this kind of variation. Comparative material of this genus includes *atrata* (1 specimen) and *sebae* (2 specimens).

Purely for purposes of vertebral identification, the New World natricines may be separated into two groups, based largely on the relative heights of the neural spine. Group I: vertebrae with a long centrum, and a low, long neural spine. The genera are usually rather small in total length. The group includes at least the following genera: *Haldea, Tropidoclonion, Seminatrix,* and *Storeria.* Group II: vertebrae with a moderate to long centrum, and a much higher neural spine than is found in Group I. The snakes in this group usually attain a greater adult size. It includes at least the following genera: *Natrix, Thamnophis, Liodytes,* and *Helicops* for those who wish to place this genus in the Natricinae.

Some species of *Natrix* (*septemvittata, rigida,* and *grahami*) might be considered intermediate in all of these characters.

Group I is composed of a somewhat varied assemblage of genera. Thus, *Storeria* apparently is characterized by a very long centrum and a high, narrow neural arch. *Haldea, Seminatrix,* and *Tropidoclonion,* in that order, approach the characteristics of Group II. The latter can be subdivided further into at least four groups. (a) *Liodytes-Helicops,* a group in which at least many specimens have the neural spine "ground-off" at the upper edge, particularly in the adults. (b) *Natrix rhombifera - taxispilota - cyclopion,* a group characterized by their large adult size, and by their very high neural spine, which is usually overhanging anteriorly in *cyclopion,* less so in *taxispilota* and *rhombifera,* especially in large specimens. (c) *Natrix sipedon-Thamnophis,* a group having a lower neural spine than subgroup (b), approaching *Tropidoclonion,* in *Thamnophis radix* and *T. brachystoma. Natrix erythrogastor* may belong to this group, but in this species the neural spine leans anteriorly more than it does in any other species of *Natrix* I have seen. (d) *Natrix septemvittata-rigida-grahami-harteri-natrix-stolata* and *tesselatus.* These species seem to form a group intermediate between those of Groups I and II, possessing long, low neural spines, but having shorter centra than in Group I. They are also intermediate in adult size between the extremes of Groups I and II.

The outline given above is not meant to convey phyletic concepts, but is added to aid in identifying snake vertebrae. There is, however, a suggestion in the groupings that seems to reflect relationship. Perhaps a more comprehensive examination of the vertebral types or skulls in this subfamily may shed considerable additional light on the relationships of the New World Natricinae as they are now defined.

Storeria cf. *S. dekayi* Holbrook

Description.—Centrum long, somewhat cylindrical to subtriangular from below, provided with a typical natricine hypapophysis on the ventral surface of each vertebra. The subcentral ridges are well developed, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, oblique. Paradiapophyses with two articular facets. The parapophysial process is projected considerably anteriorly. The cotyle is rounded, but with two small projections at the ventral lip. The neural canal is large. The neural arch is very high, without epizygapophysial spines, or if present, faint. Neural spine longer than high, with overhanging anterior and posterior edges. The zygosphene is crenate from above, somewhat angular from the front. The prezygapophysial articular facets are oval in outline. The accessory processes are short.

Fossils representing this genus are now known from only a few Pleistocene localities in Florida. There are approximately forty vertebrae known from Reddick I, B. (UF 5047-8, 6241, 5045), two from Arredondo I, A. (UF 6223 and 5922) and one (UF 6222) from Mefford Cave. The genus has never been reported before in the fossil record.

The vertebrae of *Seminatrix* and *Haldea* are similar to those of *Storeria.* From the former the fossils differ in possessing a longer centrum. From *Haldea* the fossil vertebrae may be separated by the ratio nlu/zw, in which there is no apparent overlap (at least in the middle precaudal vertebrae) (Table 21). The fossil vertebrae from Reddick possess vertebral ratios practically identical to those found in *Storeria.* and are thus placed in this genus.

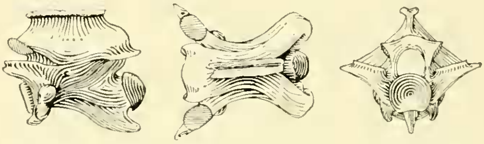

Figure 40. A precaudal vertebra of *Storeria dekayi* (UF 6241) Reddick I B, Pleistocene (Illinoian ?).

Examination of the vertebrae of *Storeria d. dekayi, S. d. victa, S. d. wrightorum, S. o. occipitomaculata* and *S. o. obscura* indicates that vertebrae of these forms apparently are difficult to separate on the basis of present knowledge. However, a comparison of the ratios of only the *middle* precaudal vertebrae of the two modern species and those of the fossils, indicates that the latter are, in all probability, *Storeria dekayi.* However, it should be pointed out that this comparison is only as good as the ability to distinguish middle precaudal vertebrae among the disassociated fossils. If *all* of the vertebrae of both the modern species and the fossils are tabulated a considerable overlap in ratios is found. Of particular importance is that there is then an extensive overlap with *Haldea* as well. Thus, at least *Storeria dekayi* is represented in the fossil sample. The absence of either *Haldea* or *Storeria occipitomaculata* is not assured. Figure 40 illustrates a fossil specimen of *Storeria dekayi* from Reddick, Florida. Table 21 compares the vertebral ratios in the two modern species of *Storeria, Haldea* and the fossil vertebrae.

TABLE 21.

A comparison of the vertebral ratios in Storeria, Haldea and the available fossil vertebrae

Ratios	*S. d.** (N=28)	*S. o.** (N=16)	*Storeria* (N=44)	*Haldea* (N=45)	Fossils (N=30)
po-pr/pr-pr	1.11-1.22	1.05-1.10	1.05-1.22	1.00-1.28	1.10-1.15
nlu/zw	1.23-1.36	1.60-1.64	1.23-1.64	1.06-1.20	1.33-1.57
nlu-nh	3.23-3.66	5.00-5.54	3.23-5.54	3.70-5.70	3.44-4.44
cl/naw	1.86-2.10	1.81-1.97	1.81-2.10	1.63-2.12	1.72-2.01

* *S. d.=Storeria dekayi* *S. o.=Storeria occipitomaculata*

Liodytes alleni Garman

Description.—Centrum moderate in length, provided with a well developed hypapophysis. Subcentral ridges strong, extending from the posterior lower edge of the diapophysis posteriorly to the condylus. Condylus on a short neck, very slightly oblique. Paradiapophysial articular facets well separated. The parapophysial process projects noticeably below, and in front of the centrum. The neural arch is moderate in height and width. Epizygapophysial spines are faint to strongly developed. Neural spine nearly as high as long, with the upper edge frequently "ground-off" in adult specimens. Zygosphene thin dorso-ventrally, crenate to convex from above, convex from the front. Prezygapophysial articular facets oval. Accessory processes lateral to slightly anterior from above, acute to somewhat obtuse, laterally directed from above.

The "ground-off" neural spine in some specimens of this species will separate them clearly from all other natricines of similar vertebral type. The presence of such vertebrae in a fossil deposit provides sufficient evidence for stating that this form occurs in the fossiliferous beds. In the xenodontine (?) genus *Helicops,* which has similar vertebrae, the epizygapophysial spines are much reduced compared with those of *Liodytes.* In addition, the neural spine is not as obviously "ground-off." There is some evidence that a neural spine of this type is variable in at least *Storeria dekayi.* The character may be sexually dimorphic in some genera (*Ninia*), ontogenetically variable in all genera in which it occurs, and a pathologic condition in individuals of many species in various families of snakes. Fossil or modern specimens lacking this peculiar neural spine would be readily confused with *Natrix sipedon.* However, the latter attains a much larger size.

Liodytes has not been reported as a fossil previously. Fossil vertebrae from Florida referred to this genus are available from the following localities: Winter Beach Locality. UF 5520, 5536 (2). Itchtuckanee Springs I. UF 5404, 5394, 5381, 5309, 5396, 5318, CMNH, Pr. 366.

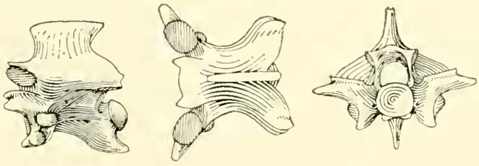

Figure 41. A precaudal vertebra of *Liodytes alleni* (UF 5536) Winter Beach-Luther Locality, Late Pleistocene ?

Figure 41 illustrates a middle dorsal vertebra of this species.

Natrix Laurenti

Description.—Centrum moderate in length, provided with a well developed hypapophysis. Subcentral ridges strong, extending from the posterior, lower edge of the diapophysis to near the condylus. Condylus on a short neck, slightly oblique. Paradiapophysial articular facets well separated. The parapophysial process is projected considerably below and anterior to the lower lip of the cotyle. The neural arch is moderate in height and width. The epizygapophysial spines usually are well developed. The neural spine is variable in height and length, never "ground-off," except in pathological individuals. Zygosphene thin dorso-ventrally, crenate, convex or straight from above, convex to straight from the front. Prezygapophysial articular facets oval to obovate. Accessory processes fairly long, acuminate to acute, directed laterally to slightly anterior from above, laterally from the front.

Numerous moderate to large-sized vertebrae are found in the Pleistocene and the Pleistocene and/or Recent deposits of Florida which are referrable to this genus. Vertebrae of *Thamnophis* apparently can be separated from those of most species of *Natrix* on the basis of the ratio cl/naw (*Natrix* 0.96-1.41, *Thamnophis* 1.36-1.99). The flattened upper edge of the neural spine apparently distinguishes most adult specimens of *Liodytes* from both *Thamnophis* and *Natrix.*

Among the fossils from Florida are a large number of moderate to very large vertebrae which possess relatively higher neural spines than occur in any natricine, with the exception of *Natrix cyclopion, N. rhombifera,* and *N. taxispilota.* One of these three species, *cyclopion,* can be separated in the majority of cases by the presence of an overhanging anterior edge on the neural spine. In *taxispilota* and *rhombifera* the anterior edge is generally straight. However, there is at least some variation in this character along the centrum and not all of the vertebrae can be assigned definitely to either spe-

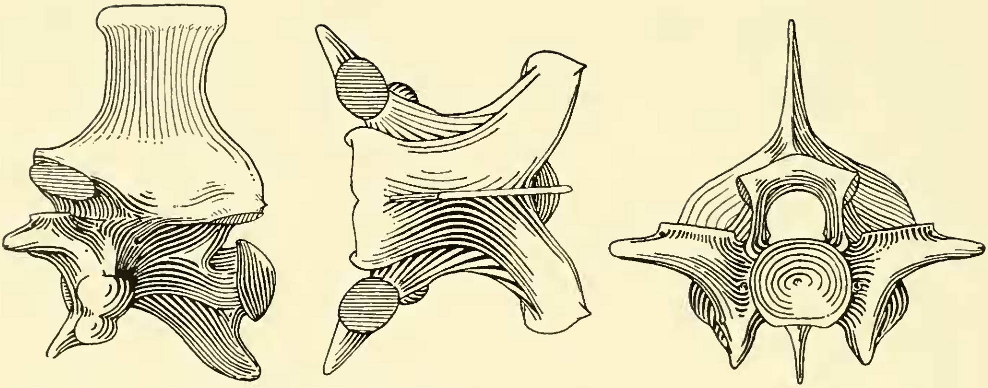

Figure 42. A precaudal vertebra of *Natrix cyclopion* (UF 4292) Itchtuckanee Springs A, Pleistocene and/or Recent.

cies. If only extremes are taken into consideration the presence of these species in a deposit can be determined fairly readily. Both types are now known from deposits in Florida.

Natrix cyclopion Dumeril and Bibron

Description.—Centrum moderate in length, subtriangular when seen from below, provided with well developed subcentral ridges, extending from the diapophyses posteriorly to the condylus. Condylus on a short neck, moderately oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial process projected anteriorly well beyond the level of the lower lip of the cotyle; cotyle rounded. Neural arch moderate in height and width, wider in larger specimens. Epizygapophysial spines usually well developed. Neural spine high, short, with overhanging posterior and anterior edges. Zygosphene thin dorso-ventrally, crenate to convex from above, convex from the front. Prezygapophysial articular facets oval to obovate. Accessory process well developed, long, acuminate to acute, directed laterally from above, laterally from the front.

This species has not been reported as a fossil previously. Fossil specimens are known from the following Pleistocene localities: Haile I, A. UF 5471, 5814. Bradenton Field A. UF 5910.

In addition, a number of specimens are known from several deposits at Itchtuckanee Springs, a Pleistocene and/or Recent locality: Locality A. UF 4281-6, 4292, 5926, 5354, 5286, 5255, all vertebrae. One maxillary (UF 4287) from the same locality is tentatively assigned to this species. Jug Springs Locality. UF 5850, 5854, 5862, 5867, 5884, 5887, all vertebrae.

One vertebra of this species is illustrated in Figure 42. Table 22 compares the vertebral ratios of modern and Pleistocene specimens of this species with modern and Pleistocene vertebrae of *Natrix taxispilota.*

Natrix taxispilota Holbrook

Description.—Centrum moderate in length, subtriangular when seen from below. pro-

TABLE 22.

A comparison of certain vertebral ratios in modern and fossil vertebrae of Natrix cyclopion and Natrix taxispilota

	Natrix cyclopion		*Natrix taxispilota*	
Ratios	Recent (N=45)	Pleistocene (N=50)	Recent (N=40)	Pleistocene (N=43)
cl/naw	1.01-1.21	1.05-1.15	0.93-1.17	1.00-1.19
naw/pr-po	1.18-1.34	1.23-1.30	1.08-1.27	1.10-1.23
nlu/nls	1.28-1.43	1.25-1.33	1.38-1.44	1.32-1.41
nlu/nh	0.85-1.12	0.92-1.08	0.75-1.09	0.86-1.10
naw/nah	1.42-1.55	1.46-1.50	1.38-1.71	1.42-1.63
pr-pr/po-pr	1.08-1.23	1.11-1.24	1.00-1.17	1.04-1.21
naw/zw	1.00-1.09	1.05-1.09	1.00-1.11	1.02-1.09
cl/zw	1.08-1.36	1.11-1.27	1.12-1.36	1.06-1.30

vided with well developed subcentral ridges extending from the diapophyses posteriorly to the condylus. Condylus on a short neck, moderately oblique to very slightly oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial articular surfaces well separated. The parapophysial process is projected strongly below and anterior to the lower lip of the cotyle. Cotyle rounded. Neural spine high, short, with a straight anterior edge, overhanging posteriorly. In small specimens of *N. cyclopion* the anterior edge of the neural spine may be straight, as in most specimens of *taxispilota.* Zygosphene thin dorsoventrally, crenate to convex from above, convex from the front. Prezygapophysial articular facets oval to obovate. Accessory processes well developed, long, acuminate to acute, directed laterally from above and from the front.

This species has not been reported as a fossil. Fossil specimens are known from the following Pleistocene localities: Haile 1, A. UF 5474, 5483, 5510, 6324, 5493, 5556, 6164, 5811, 5816.

In addition a number of specimens are known from the Itchtuckanee River area, as follows: Locality A. UF 5344, 5221, 5216, 6191, 4305, 5379, 4295, 5391, 6495, 5444, 5254, 5228, 5390, 5283, 5250, 4298, CNHM, PR. 363.

A single middle precaudal vertebra is illustrated in Figure 43. Table 22 compares the vertebral ratios of modern and Pleistocene specimens of this species with modern and Pleistocene vertebrae of *Natrix cyclopion.*

In addition to the specimens listed above under *N. taxispilota* and *N. cyclopion,* the following specimens represent one or the other species, but they are too fragmentary for exact determination: Pleistocene: Haile I, A. UF 5504, 5522. Pleistocene and/or Recent: Itchtuckanee Springs, Locality A. UF 5272, 5343, 5413, 5249, 5257, 5393, 5365, 5330, 5288, 5253. Jug Springs Locality. UF 5888, 5892.

Natrix erythrogaster Forster

Description.—Centrum moderate in length, subtriangular when seen from below, provided with well developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, moderately oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial articular facets well separated. The parapophysial process is projected strongly below and anterior to the lower lip of the cotyle. Cotyle round. Neural arch moderate in height and width, wider in large specimens. Epizygapophysial spines usually well developed. Neural spine high, short, with a straight anterior edge (rarely overhanging), leaning anteriorly, slightly higher than long, overhanging posteriorly. Zygosphene thin dorsoventrally, crenate to convex from above, convex from the front. Prezygapophysial facets oval to obovate. Accessory processes well developed, long, acuminate to acute, directed laterally from above and from the front.

On the basis of the available comparative specimens the vertebral ratios of *N. erythrogaster* and *N. sipedon* are practically identical. However, in the former the neural spine usually leans anteriorly, whereas it is perpendicular to the main axis of the cen-

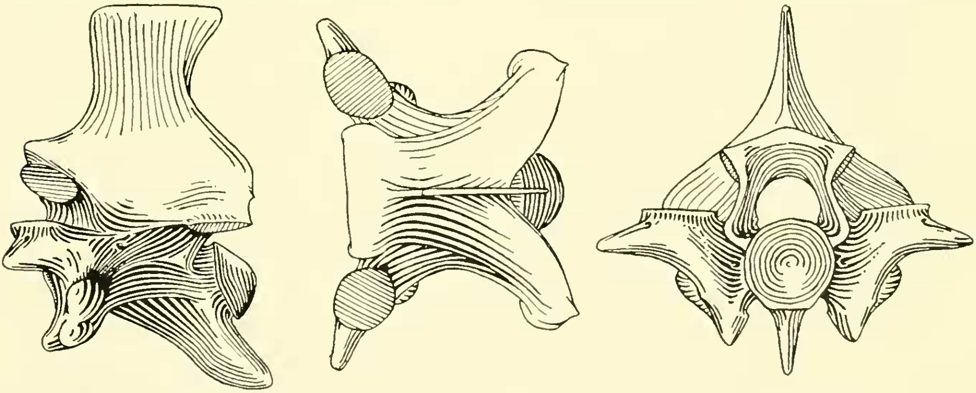

Figure 43. A precaudal vertebra of *Natrix taxispilota* (UF 5391) Itchtuckanee Springs A, Pleistocene and/or Recent.

trum in *N. sipedon.* Not every individual vertebra can be assigned with certainty to one or the other species, since considerable variation occurs throughout the column, and from one individual to the next. However, by taking the extremes the presence or absence of either species usually can be demonstrated for each fossil sample.

Only a few isolated vertebrae have been found in Florida which are referrable to this species. These specimens all come from the same locality, Haile I, A. (UF 5559, 5038). The species has not been reported as a fossil previously.

Figure 44 illustrates one of the fossil vertebrae of this species.

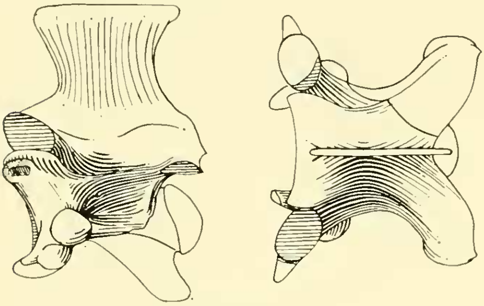

Figure 44. A precaudal vertebra referred to *Natrix* cf. *erythrogaster* (UF 5038) Haile I A, Pleistocene.

Natrix sipedon Linnaeus

Description.—Centrum moderate in length, subtriangular when seen from below, provided with well developed subcentral ridges, extending from the diapophysis posteriorly to near the condylus. Condylus on a short neck, moderately oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial articular facets well separated. The parapophysial process projected strongly below and anterior to the lower lip of the cotyle. Cotyle round. Neural arch moderate, wider in larger specimens. Epizygapophysial spines usually well developed. Neural spine approximately as high as long, more or less perpendicular to the main axis of the centrum, overhanging posteriorly, rarely anteriorly. Zygosphene thin dorso-ventrally, crenate to convex from above, convex from the front. Prezygapophysial facets oval to obovate. Accessory process well developed, long, acuminate to acute, directed laterally from both above and from the front.

This species is most easily confused with *Natrix erythrogaster.* Most vertebrae can be separated on the basis of the shape of the neural spine. In *sipedon* the spine is directed upwards, rarely anteriorly. In *erythrogaster* the spine is directed anteriorly, that is, it appears to lean forward. A fossil vertebra of *erythrogaster* is illustrated in Figure 44. An isolated vertebra of *N. sipedon* is illustrated in Figure 45. Table 23 compares the vertebral ratios of modern and fossil vertebrae of *Natrix sipedon.*

TABLE 23.
A comparison of certain vertebral ratios of Recent and Pleistocene vertebrae of Natrix sipedon

Ratios	Recent (N=60)	Pleistocene (N=21)
cl/naw	1.21-1.49	1.26-1.33
nlu/nls	1.09-1.36	1.28-1.32
pr-pr/po-pr	1.18-1.34	1.28-1.31
naw/zw	1.03-1.09	1.06-1.10
cl/zw	1.18-1.41	1.23-1.36
nlu/nh	1.29-1.62	1.37-1.53
naw/po-pr	1.05-1.18	1.12-1.19
naw/nah	1.28-1.40	1.32-1.38

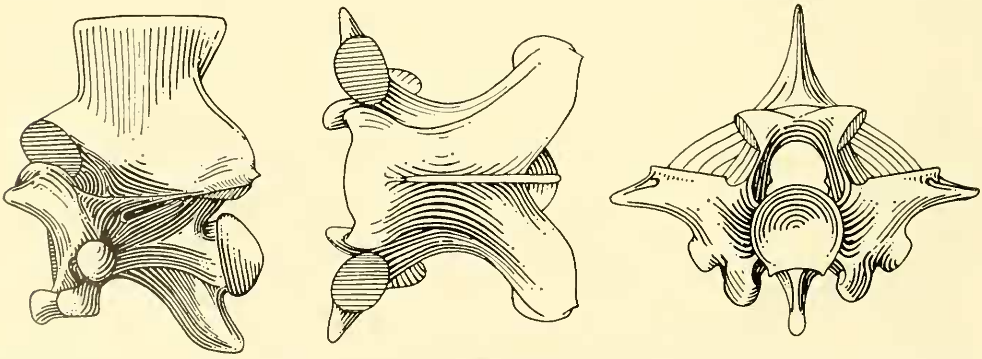

Figure 45. A precaudal vertebra of *Natrix sipedon* (UF 9867) Haile VII A, Pleistocene (Illinoian ?).

Isolated vertebrae of this species are known from the following localities: Pleistocene: Haile I, A. UF 5033, 5468, 5478, 5491, 5550, 5541, 5815, 6318. Arredondo I, A. UF 6060-1. Haile VII, A. UF 9867. Saber Tooth Cave. FGS V-5717 (Holman, 1958).

In addition, a number of vertebrae assigned to this species are known from the various localities at Itchtuckanee Springs, a Pleistocene and or Recent series of deposits: Locality A. UF 4297, 4304, 4299, 4296, 4306, 5363, 5430, 5373, 5296, 5292, 5352, 5327, 5387, 5243, 6252. Jug Springs Locality. UF 5857, 5855.

A small series of specimens (UF 6453) is known also from Hornsby Springs.

Thamnophis Fitzinger

Description.—Centrum long, subtriangular from below, provided with well developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, slightly oblique. Hypapophyses strongly developed, and sigmoid-shaped from the side. Paradiapophysial articular facets well separated. The parapophysial process is projected strongly below and anterior to the lower lip of the cotyle. Cotyle rounded. Neural arch moderate to low. Epizygapophysial spine usually well developed. Neural spine longer than high, to as long as high, overhanging anteriorly or not, always overhanging posteriorly. Prezygapophysial articular facets oval to obovate. Accessory processes well developed, long, acuminate to obtuse, directed laterally to slightly downward from the front.

Unfortunately, not only is there a general lack of comparative material of the species composing this genus, but from the available material, obviously many species cannot be separated on vertebral characters alone. However, the fossil elements from Florida can be separated from the *radix* group in having a neural spine which is higher than in that group. From *Thamnophis sauritus* they can be separated on the basis of the ratio cl/naw (*sauritus* 1.20-1.33; fossils 1.62-1.81). *Thamnophis cyrtopsis* also possesses a shorter centrum than do the fossils from Florida (cl/naw = 1.13-1.23 in *T. cyrtopsis*). The fossil vertebrae cannot be separated from *T. sirtalis*. On the other hand, *T. sirtalis* does not seem to be separable on vertebral characters alone from the remaining species in the genus not mentioned above. The fossil vertebrae from Florida are referred to *sirtalis* on zoogeographic grounds.

Thamnophis cf. *T. sirtalis* Linnaeus

Because of the similarity of the vertebrae of species in this genus a separate description of the vertebrae of *T. sirtalis* is not given. Reference should be made to the generic description.

A large number of isolated vertebrae are known from two localities within the state that are referred to this species. One of these localities is Pleistocene, and the other Pleistocene and or Recent. Isolated vertebrae occur in a number of localities in the state. Pleistocene: Reddick I, B. Approximately 50 vertebrae, UF 6040-1, 6115, 6110, 5802, 6402, 5106, 6039, 5166, 6042, 6138, 5167, 6258, 6095, 6312, 6073, 6016, 6345. Payne's Prairie B. UF 5755. Mefford Cave I. UF 2555. Arredondo I, A. UF 4294. Arredondo II, A. UF 2074. Winter Beach. UF 5834. Haile VII, A. UF 5182, 5199, 5147, 6089. Bradenton A. UF 5913. Williston, FGS V-5806 (Holman, 1959). Pleistocene and/or Recent: Itchtuckanee Springs A. UF 6493, CNHM, P.R. 370. Hornsby Springs, UF 6268.

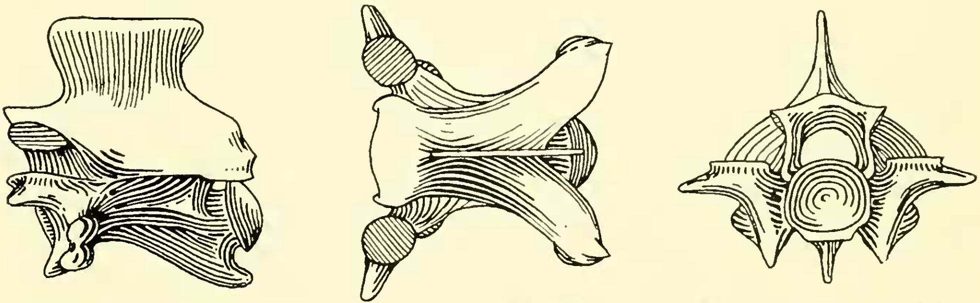

Figure 46. A precaudal vertebra of *Thamnophis sirtalis* (UF 6402) Reddick I B, Pleistocene (Illinoian ?).

A middle precaudal vertebrae is illustrated in Figure 46. Table 24 compares both fossil and modern vertebrae of *Thamnophis sirtalis.*

TABLE 24.
A comparison of certain vertebral ratios in Recent and Pleistocene vertebrae of Thamnophis sirtalis

Ratios	Recent (N=52)	Pleistocene (N=29)
cl/naw	1.60-1.80	1.62-1.81
pr-pr/po-pr	1.00-1.05	1.01-1.06
zw/naw	1.03-1.11	1.03-1.12
cl/zw	1.47-1.66	1.50-1.62
nlu/nh	1.52-1.83	1.47-1.78

Many hundreds of vertebrae, obviously representing various genera of the Natricinae are represented in the collections. However, to list these would serve no real purpose, since in no case is more than a generic identification possible. Undoubtedly, with further study, especially of vertebrae from the Reddick I, B. locality, *Haldea,* and perhaps some of the smaller species of *Natrix* will be found. There are, as yet, no vertebrae which indicate definitely the presence of species other than those described above.

F. *Family Elapidae*

Description.—Hypapophyses well developed throughout the vertebral column, straight, not as sigmoid-shaped as in the Natricinae, strongly compressed, pointed, directed posteriorly. Centrum long, with subcentral ridges well developed. Condylus on a short to moderate neck, moderately oblique. Cotyle rounded to oval. Paradiapophyses well developed, with the articular surfaces well separated, with the parapophysial process projected downwards and forwards, well beyond the lower lip of the cotyle. Neural arch usually depressed, without epizygapophysial spines. Neural spine low, long, to as high as long. Anterior edge overhanging or straight. Posterior edge always overhanging, except in a few burrowing forms. Zygosphene thin dorso-ventrally, crenate, straight or convex from above, convex to straight from the front. Maxillary poison teeth fixed in position, grooved or hollow, with or without additional posterior maxillary teeth, which are not specialized to conduct poison.

Vertebrae of the following genera have been examined: *Micrurus, Naja, Bungarus, Dendroaspis, Notechis, Haemachatus, Denisonia,* and *Ophiophagus.* In addition, the vertebrae of three genera of Hydrophidae have been examined: *Hydrophis, Laticauda,* and *Pelamis.* The vertebrae of the hydrophid snakes, though generally shorter and higher than most elapids, are similar to the latter, and if occurring as fossils probably would be placed in the family Elapidae.

Most elapid snakes possess vertebrae that vary slightly from the general description given above. However, *Bungarus* deserves special mention. In this genus the vertebrae are somewhat unusual in that the accessory processes have developed laterally into broad, flattened structures. As far as I am aware this is absent in genera belonging to other snake families, with the exception of certain xenodermines among the Colubridae.

Fossil elapids from Florida are represented by vertebrae and various portions of the skull and mandible. These constitute the first record of the Elapidae as fossils in the New World. The long, low, narrow centrum, low haemal spine and small size of these fossils all suggest a reference to genera such as *Micruroides* or *Micrurus.* The absence of any non-conducting teeth behind the enlarged fang on the maxillary suggests that at least the Pleistocene fossils represent the genus *Micrurus,* rather than the other American elapids, *Micruoides* and *Leptomicrurus.* In addition to the Pleistocene remains, one fragmentary vertebra from the Pliocene locality of Haile VI, A is tentatively referred to the genus *Micrurus.*

Micrurus Linnaeus

Description.—Each maxillary with one, or rarely two functional poison fangs, with no auxiliary teeth behind the fang, which is erect and fixed.

Middle precaudal vertebrae of typical small elapid type, with very slightly compressed, fairly straight, pointed hypapophyses, extending the entire length of the centrum. Centrum long, low, narrow, somewhat cylindrical, with strong subcentral ridges; cotyle rounded, with or without emarginated lower edge, Condyle directed more posteriorly than dorsally. Paradiapophyses well developed, parapophysial articular facets are oval to obovate. The accessory processes are acute, moderately long, directed laterally from above and from the front. Neural arch low, long, without epizygapophysial spines. Neural spine very low, long, usually with a straight anterior edge; posterior edge overhanging, at least slightly. Zygosphene convex from above, and from the front.

The vertebral columns of the following species of *Micrurus* were examined: *M. circinnalis* (1), *M. frontalis* (1), *M. corralinus* (1), *M. fulvius* (12), and *M. n. nigrocinctus* (1). Comparison of the actual vertebrae and the vertebral ratios of the several forms listed above show a close similarity among the species.

Micrurus sp.

One fragmentary vertebra (UF 9676) from the Pliocene locality of Haile VI, A is tentatively assigned to this genus. The hypapophysis, though broken, is provided with a long base and directed posteriorly as in the Recent genus. In addition, the centrum is long and the neural spine long and low. The latter is, however, higher than in most vertebrae of Pleistocene or Recent specimens of *Micrurus fulvius*. Although seemingly distinctive in this feature, description of this form as a new species is delayed until more complete material becomes available.

Micrurus cf. *M. fulvius* Linnaeus

The fossil *Micrurus* from the Florida Pleistocene cannot be assigned to any particular species with any degree of certainty, since all of the species of the genus are so similar. However, on zoogeographical grounds, as well as the composition of the remaining Pleistocene snake fauna of Florida, a tentative assignment to *fulvius* seems warranted.

Vertebrae of fossil coral snakes are known from the following localities in the state, all Pleistocene: Haile VIII, A. UF 6211, 6303 (4). Saber Tooth Cave U-5727 (Holman, 1958). Arredondo I, A. UF 6059, 6062. Williston FGS V-5808 (Holman, 1959). Reddick I, B. UF 6135 (64), 6136 (3), 6336, 6082 (80), 6178 (6), 4312, 5215 (20 vertebrae, all from the same specimen), 5311 (6 vertebrae, all from the same specimen), 6181-2, 5917 (1 complete maxillary with poison fang in place, and 1 complete surangular, from the same specimen), 5918 (the posterior portion of a cranium), MCZ 7608 (a few vertebrae and CHNM, P.R. No. 372 (a few vertebra).

About 200 vertebrae of this genus are now available from Florida Pleistocene deposits. A typical middle precaudal vertebra is illustrated in figure 47. Table 25 compares the range of variation in certain ratios obtained from six Recent specimens of *Micrurus fulvius fulvius* with the same ratios in 63 vertebrae from the Reddick Locality. The mandibular and cranial elements are identical to those found in *M f. fulvius*.

TABLE 25.
Comparison of vertebral ratios in modern and Pleistocene vertebrae of Micrurus fulvius

Ratios	Recent (N=53)	Pleistocene (N=60)
cl/naw	1.48-1.81	1.31-6.60
cl/col	5.46-6.29	4.24-6.60
ctw/cth	0.98-1.04	0.96-1.12
pr-pr/po-pr	1.01-1.07	0.95-1.08
naw/zw	0.92-1.16	0.94-1.22
cl/zw	1.49-1.74	1.45-1.93
nlu/nh	3.41-4.04	3.06-3.78

G. *Family Viperidae*

Description.—Centrum short, with well developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus large, on a short neck, directed posteriorly. Paradiapophysial articular

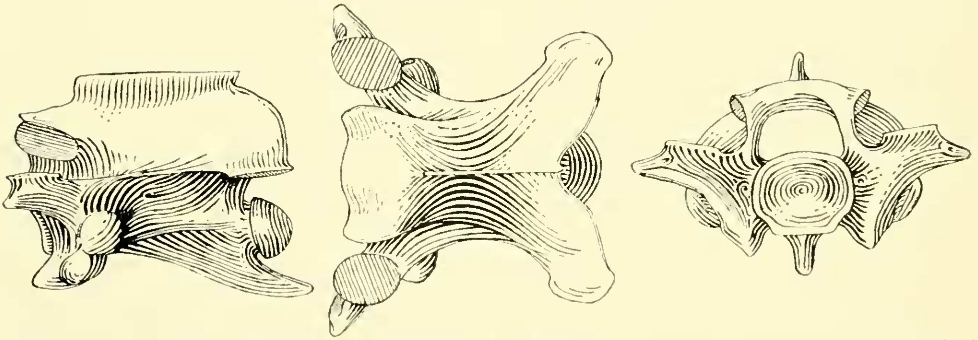

Figure 47. A precaudal vertebra referred to *Micrurus* cf. *fulvius* (UF 6135) Reddick I B, Pleistocene (Illinoian ?).

facets well separated, the parapophysial process projected anteriorly and ventrally, well beyond the lower lip of the cotyle. Hypapophyses long, not compressed laterally, straight, on all of the vertebrae, sometimes thickened distally. Cotyle obviously oval to round, depending on age and/or position in the column. Neural arch wide, short, depressed, sometimes with epizygapophysial spines. Neural spine from slightly longer than high to much higher than long, either straight at the anterior edge or overhanging, usually overhanging posteriorly. Zygosphene thin to somewhat thickened dorsoventrally, crenate or angular from the front. Prezygapophysial articular surfaces oval, obovate or subtriangular. Accessory processes not well developed, hardly projecting beyond the outer margins of the prezygapophysial articular facets.

Vertebrae of the following genera were examined: *Azemiops, Agkistrodon, Bitis, Bothrops, Causus, Crotalus, Sistrurus, Trimeresurus*, and *Vipera*.

Among the viperines, the genus *Vipera* seems most distinctive. The vertebrae are longer than in the other genera examined. The neural spine is lower than in most, and epizygapophysial spines are fairly well developed. These characters are somewhat approached by *Causus*. There is a tendency in the Viperinae for the hypapophysis to be proportionately shorter than it is in the Crotalinae. However, *Bitis arietans* approaches the condition found in the Crotalinae, since the hypapophyses in this genus are fairly long.

The fossil viperid vertebrae from Florida most certainly represent the Crotalinae rather than the Viperinae. Comparative material of Recent forms in the Crotalinae includes the following: *Agkistrodon halys* (1), *A. contortrix* (4), *A. piscivorus* (8), *A. bilineatus* (1), *Bothrops atrox* (3), *B. jararacussu* (1), *B. schlegelii* (2), *B. neuweidii* (3), *B. alternata* (1), *Crotalus adamanteus* (8), *C. horridus* (4), *C. ruber* (1), *C. atrox* (2), *C. mitchelli* (1), *C. tigris* (1), *C. durissus* (2), *C. molossus* (1), *Sistrurus miliarius* (6), *S. catenatus* (3), and *Trimeresurus viridisoma* (1).

A variety of vertebral types are found in this subfamily. The genus *Bothrops*, for example, is made up of at least two groups on the basis of vertebral form. In *Bothrops schlegelii* the vertebrae are much longer in proportion to their width than in any of the other species examined. The vertebrae of *B. atrox* and *B. neuweidii* are somewhat intermediate. The remaining species examined have much wider vertebrae in proportion to their length. *Bothrops schlegelii* approaches the condition found in *Trimeresurus, Agkistrodon,* and *Sistrurus;* genera in which the vertebrae are usually somewhat lengthened. In *Agkistrodon, A. contortrix* possesses a longer vertebra than *A. piscivorus* and *A. bilineatus*, the latter being somewhat intermediate between the two other species. The genus *Crotalus* seems to be composed of species all of which possess short centra. However, the more primitive species, *triseriatus* and related forms, have not been examined, and perhaps they too possess the longer vertebrae observed in other genera in this subfamily.

Among the Pleistocene fossil viperid remains from Florida, there are a large number of vertebrae which have a rather long centrum, a proportionately low neural spine, and all of moderate size, which certainly seem to represent the genus *Sistrurus*. They can be separated from vertebrae of *Bothrops schlegelii* in centrum length and in that they possess higher neural spines; from *Trimeresurus* by the much more projected lower diapophysial process; from *Agkistrodon* and *Crotalus*, as well as the remaining species of *Bothrops*, by their longer centrum.

Sistrurus Garman

Description.—Vertebrae of typical basic viperid type; *i.e.*, with long, straight hypapophyses, directed downward more than backward. Subcentral ridges strongly developed, extending from the diapophyses to the condylus. Parapophysial process strongly developed, greatly projected anteriorly and downward, beyond the lower lip of the cotyle. Paradiapophyses with well developed articular surfaces, separated, the diapophysial member much more obviously rounded. Cotyle almost always round. Condylus on a short neck, only slightly oblique. Neural arch moderately depressed, long, with or without faint epizygapophysial spines. Neural spine moderately high, approximately as high as long. Zygosphene thin dorsoventrally, convex, crenate, straight or sometimes concave from above, convex or angular from the front, sometimes with a small median tubercle, or with a small dorsally-directed process at the base of the zygosphene, just anterior to the neural spine. A keel may or may not be present on the dorsal surface of the zygosphene. Zygosphene wider than the cotyle. Prezygapophysial articular facets oval to obovate, sometimes subrectangular.

The rounded cotyle, virtual absence of epizygapophysial spines, wide zygosphene, small size, longer and narrower centrum will usually suffice to separate it from practically all other viperid snakes. In most small specimens of *Crotalus* the cotyle is oval in shape when the zygosphene is convex. In *Sistrurus* the zygosphene is convex from the front, but the cotyle is always much more rounded than oval. However, not every vertebra can be identified with certainty, especially as fossils, since correct identification depends on a perfectly preserved specimen.

The two species of *Sistrurus* available as comparative material, *catenatus* and *miliarius* have similar vertebrae. On the basis of the available skeletons, they are most easily separated by the ratios zw/cl, ctw/cth, and cl/naw. In the latter two ratios there is considerable overlap, but extremes can be identified. In the case of the former only a slight overlap appears to exist. On the basis of these three ratios the fossil vertebrae from Florida seem closer to *miliarius*, and they are assigned to this species.

Some of the fossil vertebrae exceed the size of those of Recent specimens with the possible exceptions of individuals from southern Florida. In this area, *Sistrurus miliarius* attains a greater size than in any other part of its range. This is also the population which Gloyd (1940) chose as probably representing the most primitive one of the species. The fossil vertebrae, collected mainly from central Florida, may be interpreted as supporting this general hypothesis; *i.e.,* that the Florida population of *S. miliarius* is more primitive than those to the north and west of this area. However, other factors may be responsible for the presence of somewhat larger vertebrae of this species in the Pleistocene of Florida than are found in the general area at the present time. Climate has been thought to be important in bringing about larger size in other Pleistocene snakes (Brattstrom, 1953b).

Sistrurus miliarius Linnaeus

Specimens representing this species are now known from the following localities, all Late Pleistocene: Haile VII, A. UF 6425 (3), 6427 (3), 6426 (3), 5614 (1), 6435 (27), 5189 (1). Williston, FGS V-5809 (Holman, 1959). Reddick 1, B. UF 5637 (1), 5604 (1), 6416-18 (7), 6442 (1), 6311 (1), 6441 (1), 6443 (1), 5108 (1), 6066 (1), 6051 (1), 5640 (1), CNHM, P.R. 371 (5).

Figure 48 illustrates a middle precaudal vertebra. Table 26 compares the vertebral measurements and ratios of the fossil vertebrae with those of *S. catenatus* and *S. miliarius.*

The remaining viperid vertebrae from Florida apparently belong to both *Agkistrodon* and *Crotalus.* These two genera are not always separable on vertebrae alone. However, both genera seem to be represented in the Pleistocene deposits of the state.

Agkistrodon Beauvois

The vertebrae of large specimens of both *Agkistrodon piscivorus* and *Crotalus* are sometimes difficult to separate. In *Agkistrodon piscivorus* there is a tendency for the neural spine to be lower, thinner, and without a thickening on the upper anterior edge. The hypapophysis is, in general, shorter. The parapophysis is more projected, the projections being more parallel from below; not shorter and usually more diverging as in *Crotalus.* The area between the lateral edge of the cotyle and the buttressed base of the prezygapophysis is more deeply indented in *Agkistrodon piscivorus.* The prezygapophysial articular surfaces are usually more

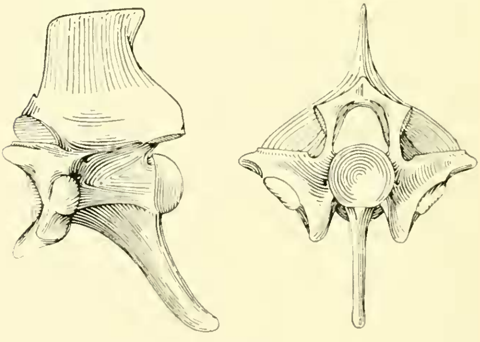

Figure 48. A precaudal vertebra of *Sistrurus miliarius* (UF 6417) Reddick I B, Pleistocene (Illinoian ?).

TABLE 26.
Comparison of vertebral measurements (in mm) and ratios in Recent specimens of Sistrurus miliarius, S. catenatus and Pleistocene vertebrae from Florida

Ratios	*Sistrurus miliarius* (N=52)	*Sistrurus catenatus* (N=25)	*Fossils* (N=20)
cl	3.28-4.19	3.28-4.14	3.35-4.70
naw	2.34-3.12	2.34-3.05	2.79-3.91
cl/naw	1.04-1.42	0.98-1.23	1.06-1.37
ctw	1.42-2.06	1.52-2.92	1.60-2.21
cth	1.40-2.03	1.45-2.87	1.78-2.29
ctw/cth	0.93-0.99	1.00-1.12	0.95-1.06
zw	2.36-3.12	2.62-4.37	2.46-2.95
zw/cl	0.67-0.76	0.78-0.94	0.59-0.79
nh	2.18-2.74	2.54-3.79	1.60-3.48
nlu	2.36-3.20	2.69-4.24	2.59-3.18
nlu/nh	1.00-1.20	1.00-1.38	0.98-1.30
pr-pr	4.78-5.40	4.50-8.84	5.44-7.72
po-pr	4.24-5.28	4.14-6.68	4.39-5.94
pr-pr/po-pr	1.10-1.24	1.09-1.35	1.11-1.21
zw/ctw	1.30-1.67	1.41-1.71	1.20-1.39

horizontally directed in *Agkistrodon* than in *Crotalus*.

I have not been able to assign, with certainty, all the fossil Florida crotaline vertebrae to either *Crotalus* or *Agkistrodon*. However, I am sure that at least a few of the vertebrae definitely represent the latter. The remaining specimens cannot be assigned, or are referred to the genus *Crotalus*. The large size of the fossils assigned to *Agkistrodon,* the shorter centrum length and the high neural spines suggest *A. piscivorus,* and not *A. contortrix*. The latter is most easily confused with *Sistrurus,* from which it can be separated most readily by its somewhat shorter centrum and the shape of the zygosphene.

Agkistrodon piscivorus Lacepede

Description.—Centrum length moderate to short, provided with strong subcentral ridges, extending from the base of the diapophyses posteriorly to near the base of the condyle. Condylus large, on a short neck, moderately oblique. Paradiapophyses well-developed, with two articular facets, occasionally with what appears to be a third directly anterior to the dorsal one. Parapophysial process strongly projected downwards and forwards, somewhat flattened, looking outwards and upwards, more or less parallel when seen from below. Cotyle slightly oval to round. Neural arch moderate in width, becoming much wider in larger specimens. Epizygapophysial spines usually faint, if present at all. Neural arch depressed. Interzygantral ridges moderate to strongly developed, strongly emarginated. Zygosphene straight, convex or with a median notch from above, rarely concave from above; straight, convex from the front. Prezygapophysial articular facets oval to subtriangular. Neural spine high, short, very thin at its anterior edge, usually leaning posteriorly, over-hanging slightly posteriorly.

This species was reported by Brattstrom (1954a) from the following localities in Florida: Seminole and Bradenton Fields and Crystal Springs, all Pleistocene and/or Recent in age. In addition, vertebrae referred to this species are now available from the following localities, all Pleistocene in age: Haile VII, A. UF 6394, 9865, 6284, 5620. Saber Tooth Cave. FGS V-5728 (Holman, 1958). Williston. FGS V-5810 (Holman, 1959). Haile I, A. UF 5499, 5508, 5466, 6323. Payne's Prairie B. UF 5753.

Figure 49 illustrates a middle precaudal vertebra of this species.

Crotalus Linnaeus

The problems involved in distinguishing the various species of *Crotalus* on the basis

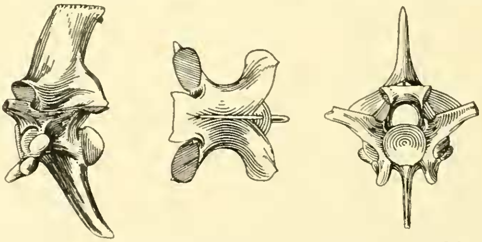

Figure 49. A precaudal vertebra of *Agkistrodon piscivorus* (UF 5733) Payne's Prairie B, Late Pleistocene.

of only their vertebrae have been more difficult for me than those encountered in separating *Agkistrodon* from *Crotalus*.[10] On the basis of the available comparative material, *C. tigris* is certainly distinctive. It is distinguished from other species in the same genus by a longer centrum and a lower neural spine. *C. mitchelli, horridus, durissus,* and *molossus* all possess precaudal vertebrae which seem shorter, broader and with lower neural spines than are found in *ruber, atrox,* and *adamanteus*, though the differences are not striking, and there is considerable overlap. *C. adamanteus* possesses very high neural spines, especially in large individuals. The parapophysial processes are frequently more strongly developed than in the remaining forms. Some of the fossil vertebrae from Florida are certainly referrable to this species, but there is no certainty that *horridus* is not also represented in the available fossil material.

Gilmore (1938) stated that except for larger size, *C. adamanteus* cannot be separated from other species on vertebral characters alone. For this reason he refers most of the fossil crotaline vertebrae from Florida to *C. adamanteus* on size alone. Hay (1917, *et al.*) assigned vertebrae to separate species, without stating on what bases the distinctions were made. One is left with the impression that most of the identifications were based on the ranges of the modern species. Brattstrom (1954a) referred the available fossil rattlesnake vertebrae to several modern species, but gave no hint of the means by which they were separated other than a reference to the ratio of log-differences of a series of analogous measurements. However, I believe this statistic is not applicable readily in distinguishing between two samples in which variation (ontogenetic, non-determinant growth, and intracolumnar) is so great. However, its use in snake vertebrae may have considerable value if the samples are known to have originated from specimens of equal size and/or age. Using the same statistic, greater differences can be demonstrated between hatchling and adult specimens of *C. adamanteus* than between adults of *adamanteus* and *horridus.*

Young rattlesnakes definitely are represented in the Florida Pleistocene, frequently to the exclusion of adults in the same deposit. Statistically validated size differences between two samples of fossil vertebrae do not indicate necessarily the presence of two or more species, but simply suggest that the samples differ in size. On the basis of the log-difference statistic Brattstrom described two new fossil rattlesnakes from Florida, *C. adamanteus pleistofloridensis* and *C. giganteus.*

According to Brattstrom (p. 35), *C. a. pleistofloridensis* differs from *C. a. adamanteus* ". . . in having a higher neural spine, a longer hypapophysis, the parapophysis longer and bent laterally, and the process of the prezygapophysis wider than the process of the postzygapophyses . . . (p. 36) . . . but especially in its larger size."

As far as I can determine, the characters which are given as diagnostic are all somehow related to total size; that is, they all seem to exhibit ontogenetic variation.

The length of the neural spine and the hypapophysis depends, in part, on the position within the vertebral column, shortest posteriorly. According to Brattstrom's figure 1, the hypapophysis of *pleistofloridensis* is not significantly longer than in *adamanteus.* Furthermore, the fossil vertebrae referred to *pleistofloridensis* by Brattstrom and measured by myself (AMNH 6776, AMNH 6778, MCZ 2101, MCZ 2112-3, USNM 11333) are not significantly larger than those from a six and a half foot living specimen from Astor Park, Lake County, Florida. Gilmore (1938: 74) stated that some of the fossil vertebrae "rival" and "are nearly as large" as those of a recent specimen in the United States National Museum that was seven feet in length. In fact, many of the vertebrae placed in *pleistofloridensis* are much smaller than those of the largest modern specimens available. The parapophysial process in a young *C. adamanteus* from Daytona Beach, Florida is pointed, proportionately short and directed upwards, not outwards. In a three and a half foot specimen from High Springs, Florida the process is longer, not as pointed, but with a rounded anterior edge, and facing outwards slightly, as well as being proportionately wider. This

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[10] According to Brattstrom (pers. comm.) some of his studies suggest that characters are now available which are not only useful in separating the precaudal vertebrae of various species of crotalids, but will position the elements within the vertebral column as well. This publication will do much to clarify what is at best described as a difficult problem at present.

trend is continued in larger specimens and becomes exaggerated in the overly large species, *C. giganteus.*

The prezygapophysis is wider than the postzygapophysis in very young rattlesnakes (po/pr 0.91), becoming equal in average-sized specimens (po/pr 1.00), and thence becoming wider again in very large specimens (po/pr 0.92).

The largest specimen of *C. adamanteus* recorded measured eight feet, nine inches (Gilmore, 1938). However, apparently this is based on Stejneger's specimen, which has since been lost, so that there is no means by which the length can be checked. There is every reason for believing that *C. a. pleistofloridensis* attained lengths of from seven to eight feet. The largest Recent specimen of *C. adamanteus* for which reliable data are available is seven feet, four inches in total length; larger than the Recent comparative material available to Gilmore and to myself. It is larger than most specimens of *pleistofloridensis.*

Larger rattlesnakes are becoming more unusual with continuing human development of the southeastern states. Large specimens of *C. adamenteus* apparently were more common during the past than at the present time. Man is certainly an important factor in reducing the number of the larger specimens found in any one area. Vertebrae collected from Indian mounds in Florida indicate that unusually large specimens were more common during that period than at the present time. Many of the specimens equal, or even exceed, the size of *C. a. pleistofloridensis.*

Based on the above, *Crotalus adamanteus pleistofloridensis* is referred to the synonymy of *Crotalus adamanteus.*

The problems involved in determining the validity of *Crotalus giganteus* are somewhat greater. This species differs from *adamanteus* in its larger size and, according to Brattstrom (1954a: 36) ". . . in having the hypapophysis widest (antero-posteriorly) at its tip and not at its base". This species may have been as long as twelve feet, considerably larger than the largest Recent *C. adamanteus.*

The hypapophysial character loses some importance when one realizes that there is at least some intra- and intervertebral variation in this character (in the anterior vertebrae the tips of the hypapophyses are generally narrower than at their bases, in the posterior vertebrae the tips may be somewhat wider). A much more important character is the ratio cl/naw. In Recent specimens examined this ratio varies from 0.79-1.08. In the type of *C. giganteus* (AMNH 6772), two very large vertebrae from Hornsby Springs (UF 6269 and UF 6281), and a series from Eichelberger Cave B (UF 6376) the ratio varies from 0.67-0.78. This difference cannot be explained easily on an ontogenetic basis, at least with the comparative material available. Therefore, for the present I think *C. giganteus* should be retained as a valid species. Figure 50 illustrates the ontogenetic change and variation of the ratio cl/naw in Recent and Pleistocene *Crotalus adamanteus* and *C. giganteus.* This ratio may also provide a means of distinguishing juvenile specimens of *giganteus* from *adamanteus,* something which was not possible before. So far, none of the smaller vertebrae referrable to *Crotalus* can be assigned clearly to *giganteus.* However, the sample of *C. giganteus* from Eichleberger Cave B contains specimens no larger than the largest specimens previously referred to *C. a. pleistofloridensis.* There is no overlap in the ratio when plotted against centrum length.

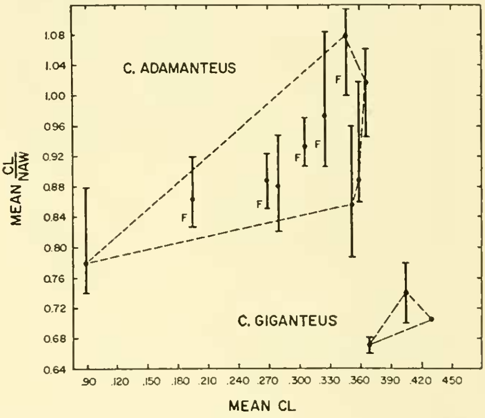

Figure 50. Ontogenetic change and comparison of the ratio cl/cw in Recent and Pleistocene *Crotalus adamanteus* and *C. giganteus,* plotted against the mean cl. Vertical bars represent the actual variation for each Recent specimen, or for each series of fossil vertebrae from one locality. The letter "F" indicates a fossil sample. The dot in the distribution of *C. giganteus* represents the holotype (AMNH 6772).

? *Crotalus*

One very fragmentary vertebra from the Pliocene locality of Haile, VI, A is tentatively referred to this genus. That the specimen represents a crotalid snake is indicated by the long, somewhat rod-like hypapophysis with parallel anterior and posterior sides, directed almost vertically, and with very short accessory processes. The snake was presumably the same size as an average specimen of *Agkistrodon piscivorus*. The vertebra is important in that it represents the earliest record of the family in eastern United States.

Crotalus adamanteus Beauvois

Description.—Centrum length moderate to short, provided with strong subcentral ridges, extending from the base of the diapophysis posteriorly to near the base of the condylus. Condyle very large, on a short neck, moderately oblique to facing directly posteriorly. Paradiapophysis well developed, with two distinct articular facets, occasionally with what appear to be a third surface directly anterior to the dorsal one. Parapophysial process strongly projected downwards and forwards, somewhat flattened, looking upwards, to upwards and outwards, diverging to just about parallel from below. Cotyle strongly oval to round. Neural arch moderate in width, wider in larger specimens, depressed. Epizygapophysial spines absent or weakly developed. Interzygapophysial ridges moderate to strongly developed, emarginated. Zygosphene straight, concave from above, sometimes with a median notch, straight or convex from the front, thin to very thickened dorso-ventrally. Prezygapophysial articular surfaces oval to decidedly rectangular. Neural spine high, narrow, usually with a tubercle on the anterior, upper edge, especially in the more anterior vertebrae, higher and narrow in the anterior vertebrae, to slightly longer than high in the posterior members.

This species was reported from a number of localities in Florida by Hay (1917, 1923), Gilmore (1938), Brattstrom (1953a, 1954a), and Holman (1958, 1959). These included the following localities: Pleistocene: Pit No. 2, Florida Lime Co. FGS V-2987. Allen Cave. AMNH 6778. Saber Tooth Cave. FGS V-5717. Williston, FGS V-5811. Pleistocene and/or Recent: Vero Beach. USNM 11333, FGS V-2414, 2411, 2399, 2412, 1702, 191, 1765, MCZ 2112-3. Seminole Field. AMNH 6776, UMMP 1009-10. Melbourne Field. USNM 13678, 13679, 13677, 11220, 11856, MCZ 2101.

To these should be added the following localities: Pleistocene: Mefford Cave. I, A. UF 2558. Eichelberger Cave B. UF 6477-9. Reddick I, B. UF 5015, 6038, 4314, 5801, 6012, 6366, 6111, 4315, 4313, 6372, 5806, 6008, 5636, 6034, 5638, 6043, 4303, 5718-9. Wall Co. Pit. UF 5717. Haile VII, A. UF 6274, 5614, 6440, 6028, 6395, 5628, 5613, 5618, 5631, 5615, 5632, 5631, 5146, 5608, 5630, 5609, 5607, 5610, 5625, 5616, 5627, 5158, 5629, 6200, 5619, 5621, 5612, 5622, 6270, 6305, 6423, 6282, 5905, 6286, 6399, 5611, 5617, 6278, 6285, 9866, 6302. Kanapaha I, A. UF 6005, 6055, 5761. Haile I, A. 5293, 5339, 5455. Haile I, B. UF 5039.

In addition, vertebrae are also available from the following new Pleistocene and/or Recent deposits: Itchtuckanee Springs: UF 5293, 5339, 5455. Haile I, B. UF 5039.

Various available cranial elements are placed in this species. They are identical to those of the Recent species in Florida. These include the following specimens: UF 6249, a replacement fang, Kanapaha I, A; UF 6342, two replacement fangs, Itchtuckanee Springs; UF 6035, a fragmental surangular, Reddick I, B; a fragmentary maxillary, Haile VII, A; UF 5207, a fragmentary maxillary, Haile I, B; UF 5120, a functional fang, Reddick I, B; UF 5125, a replacement fang, Reddick I, B.

Table 27 compares the vertebral ratios of *Crotalus adamanteus,* both Pleistocene and Recent, with *Crotalus giganteus.* Because of the similarity of these two species, except in size and centrum width, only the latter is illustrated (Fig. 51).

Crotalus giganteus Brattstrom

Description.—A large rattlesnake, characterized, besides size, by its very wide vertebrae. Centrum short, wide, with well developed subcentral ridges, extending from the diapophysis posteriorly to near the condylus. Condylus large, on a very short neck, directed posteriorly. Parapophysial processes strongly projected anteriorly and downwards, facing more laterally than dorsally, rounded at the end. Two articular facets on the paradiapophyses, with a smaller surface immediately in front of the diapophysial surface. Cotyle somewhat oval to round. Neural arch depressed, without epizygapophysial spines.

TABLE 27.
Comparison of some vertebral ratios in Crotalus adamanteus, both Pleistocene and Recent, with Crotalus giganteus

Ratios	*C. adamanteus* Pleistocene (N=60)	*C. adamanteus* Recent (N=78)	*C. giganteus* (N=8)
cl/naw	0.99-1.05	0.79-1.08	0.67-0.78
zw/cl	0.96-1.01	0.90-1.03	0.95-0.97
nlu/nh	0.68-1.15	0.63-1.10	0.54-0.81
pr-pr/po-pr	1.58-1.86	1.61-1.92	1.75-1.98
nh/cl	0.77-1.22	0.63-1.31	0.87-1.41
ctw/cth	1.00-1.17	0.98-1.21	1.00-1.04

Zygosphene thick dorso-ventrally, concave to straight from above, straight to convex from the front. Neural spine much higher than long, slightly overhanging posteriorly. Hypapophysis long, straight, with or without the tip wider than the base.

This species was described originally by Brattstrom on the basis of the two very large vertebrae from Allen Cave (AMNH 6772, 7171). As pointed out above, it differs from *C. adamanteus* in its larger size and in the wider vertebrae (Fig. 51). However, further study of larger comparative specimens of Recent *Crotalus adamanteus* and additional fossil material may show that this species should be referred to *C. adamanteus*. Vertebrae are now known from a few additional localities in Florida, as follows: Pleistocene: Haile VII, A. UF 9863. Eichelberger Cave B. UF 6376. Pleistocene and/or Recent: Hornsby Springs. UF 6269, 6281, two very fine vertebrae of this species. Rock Springs. UMMP 11013.

Figure 51 illustrates a perfect vertebra assigned to this species. Table 27 compares the vertebral ratios of this species with those of *C. adamanteus*, both fossil and Recent.

In addition to the fossil elements described and/or discussed throughout this paper, several hundred elements, mostly Pleistocene, have not been assigned to species because of their fragmentary nature. Thus, many vertebrae, not listed above, may be assigned to *Elaphe* sp., or *Natrix* sp., etc. However, these specimens have not been considered if other vertebrae from the same deposits could be correctly assigned to a certain species. Many vertebrae are so fragmentary that they can-

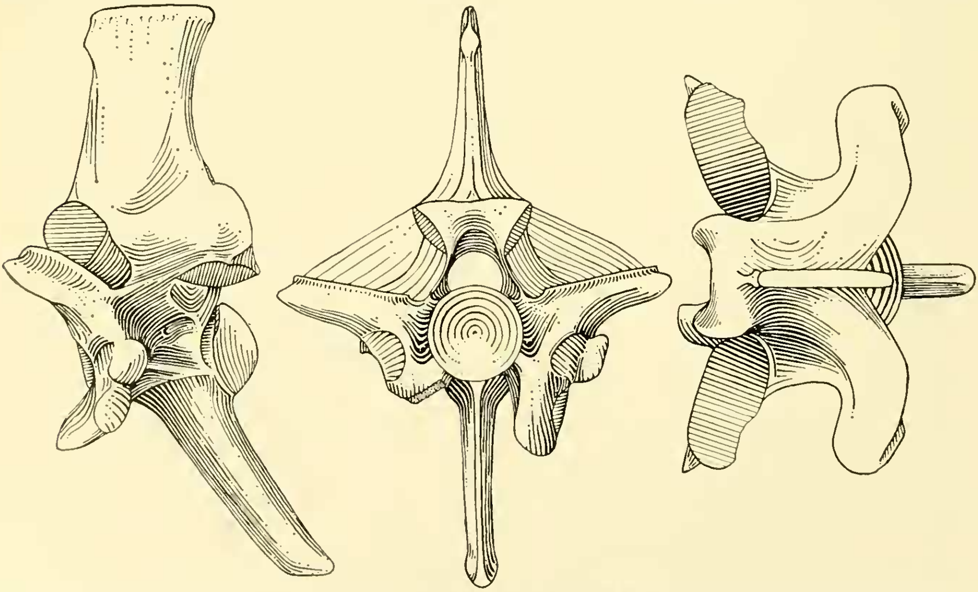

Figure 51. A precaudal vertebra of *Crotalus giganteus* (UF 6281) Hornsby Springs, Pleistocene and/or Recent.

not be assigned to even a particular genus, some not even to a particular family. For the most part, I feel that these un-assigned elements would not add greatly to either faunal or distributional patterns as now understood. Of particular interest, however, are three fragmental vertebrae (UF 6469, 6473, 6411) from the Pliocene locality of Haile VI, A. These elements undoubtedly represent a new species of colubrid snake, perhaps belonging to the genus *Elaphe,* but which, because of their fragmental nature, have not been described.

Table 28 summarizes the data on the known geological range of the families, genera and species of snakes found as fossils in Florida.

VI. DISCUSSION

The material on which this study is based contains a fair proportion of the Late Tertiary and Quaternary snake fossils of the New World, particularly in number of species. For the first time it is possible to describe from the Miocene to the present the changing snake fauna of a somewhat restricted area in reasonable detail. The record from all but the Late Pleistocene is too meager to permit evaluation of the classification of modern snakes in the light of their fossil history. This remains for the future.

In the New World the terrestrial Lower Miocene beds of Florida provide the earliest members of the Colubridae. In the Old World the earliest colubrids are also known from the Miocene (Gilmore, 1938, *et al.*). Miller (1955) placed the North American Eocene snake, *Cheilophis,* in the Colubridae, but this seems unwarranted on the basis of our present knowledge.

The family Colubridae is represented in the Lower Miocene of Florida by at least two genera, *Paraoxybelis* and *Pseudocemophora. Paraoxybelis* seems unrelated to any modern North American genus, but may be close to one of several Central and South American forms, particularly *Oxybelis.* If true, then the presence of this group in North America during the Miocene supports Dunn's view (1928) that *Oxybelis* belongs in the Colubrinae rather than the Xenodontinae. The re-establishment of the connection between the two continents during the Pliocene would have allowed *Oxybelis* and related forms to spread into South America at that time.

The remaining Miocene colubrid from Florida, *Pseudocemophora,* seems close to the modern genera *Lampropeltis* and *Cemophora,* and may be ancestral to one or both of them, thus tending to support Blanchard's hypothesis (1921) that *Lampropeltis* was derived during the Miocene.

The only other Miocene colubrid known from North America is *Dryinoides* from the upper portion of the Madison Valley formation of Wyoming (Auffenberg, 1958b). It seems close to *Conophis,* a genus which Dunn (1928) places in the Xenodontinae.

The first known fossil of the family Aniliidae is from the Cretaceous of North America (Hecht, 1959). Two species are known from the Eocene of Wyoming (Hecht, 1959). It is now known from the Florida Miocene as well. Conceivably certain other fossil snakes described from other formations in various parts of the world, placed in the Boidae at present, belong here. Unfortunately the generic relationships of the Florida fossil anilid, *Anilioides minuatus,* are unknown.

The remaining Miocene snakes of Florida are members of the family Boidae. The largest of these is *Pseudoepicrates,* a form similar to *Epicrates* and *Constrictor.* Like the former, *Pseudoepicrates* was probably equally adjusted to both an arboreal and a terrestrial existence. It may also have frequented caves and fissures in search of bats.

The end of the Miocene marks the last appearance of the larger terrestrial and arboreal boas in temperate areas of both North America and Europe (Kuhn, 1939), ending a nearly unbroken record from the Lower Eocene to the Lower Miocene on both continents.

The two remaining genera of Miocene boids found in Florida, *Calamagras* and *Ogmophis* (the latter at least in part), may be related to the Recent North American genera *Charina* and *Lichanura.* On the other hand, the suggested relationships may be the results of parallel development, in which case the relationships of the fossil forms remain obscure. In any event, the general nature of the vertebrae (small size, low neural spines, etc.) seems to suggest fossorial or semifossorial habits. On the basis of the presumed paleoecological conditions at the Thomas Farm there is doubt that the fossil

TABLE 28.
The fossil snakes of Florida and their geologic distribution

Taxa	Cret.	Paleo.	Eoc.	Olig.	Mio.	Plio.	Pleist.	Recent
Aniliidae	X		X		F			X
Anilioides minuatus +					F			
Boidae	?	X	X	X	F		X	X
Erycinae		X	X	X	F			X
Calamagras +			X	X	F			
C. floridanus +					F			
Ogmophis +				X	F			
O. pauperrimus +					F			
Boinae			X	X	F		X	X
Pseudoepicrates stanolseni +					F			
Colubridae					FX	FX	FX	FX
Colubrinae					FX	FX	FX	FX
Carphophis amoenus							FX	FX
Farancia abacura or *Abastor erythrogramus*							F	FX
Paleofarancia brevispinosus +						F		
Diadophis						F	FX	FX
D. elinorae +						F		
D. punctatus							FX	FX
Heterodon						FX	FX	FX
H. platyrhinos							FX	FX
H. simus							FX	FX
H. brevis +						F		
Opheodrys aestivus							F	FX
Coluber						X	FX	FX
C. constrictor						X	FX	FX
Masticophis							FX	FX
M. flagellum							FX	FX
Drymarchon corais							FX	FX
Elaphe						X	FX	FX
E. obsoleta							FX	FX
E. guttata							F	FX
Pituophis melanoleucus							FX	FX
Lampropeltis						X	FX	FX
L. getulus							F	FX
L. doliata							FX	FX
Stilosoma						F	F	F
S. vetustum +						F		
S. extenuatum							F (?)	F
Pseudocemophora antiqua +					F			
Tantilla coronata							F	FX
Rhadinea flavilata							F	FX
Paraoxybelis floridanus +					F			
Natricinae					X	X	FX	FX
Storeria dekayi							F	FX
Liodytes alleni							F	F
Natrix						X	FX	FX
N. cyclopion							F	FX
N. taxispilota							F	FX
N. erythrogaster							F	FX
N. sipedon							F	FX
Thamnophis						X	FX	FX
T. sirtalis							FX	FX
Elapidae					X	F	FX	FX
Micrurus fulvius							F	FX
Micrurus sp.						F		
Viperidae				X	X	FX	FX	FX
Sistrurus miliarius							F	FX
Agkistrodon						X	FX	FX
A. piscivorus							F	FX
Crotalus						FX	FX	FX
C. adamanteus							F	FX
C. giganteus +							F	
C. sp.						F		

F = Florida X = Other than Florida + = extinct taxons boids from this deposit were true leaf burrowers. Like the modern boid genus *Eryx, Ogmophis* and *Calamagras* probably burrowed in loose, dry soil.

According to Chaney (1940), climate was equable all through the Miocene, and the fossil snakes of Thomas Farm seem to suggest semi-arid tropical to subtropical conditions in a karst type topography with open shrubby vegetational community types, perhaps slightly more lush near permanent or even temporary shallow ponds, sink holes, etc.

There is every reason to believe that the modern families of snakes have a longer history than the available fossils seem to indicate. Although the relationships of some of the earlier fossil snakes have not been established definitely, the Boidae certainly extend back to the Paleocene. The fossil boids from Florida merely represent the culmination of several North American lines. The Miocene also seems to mark the last appearance of the Aniliidae in North America. The present disjunct range of the family is a phenomenon associated with the general pre-Pliocene modernization of the snake fauna of the world. The Colubridae known from the Lower Miocene of Florida indicate that this family also extends at least to the Oligocene, and probably the Eocene. The Florida Miocene species seem to represent, at least to some extent, the first stages in the deployment of higher forms represented by the Recent fauna of North America.

No terrestrial deposits of Middle or Late Miocene age are known from Florida as yet. During this period the peninsula was presumably almost completely covered by a shallow sea (Pirkle, 1957). During this time the Boidae, Aniliidae and certain members of the Colubridae apparently disappeared from eastern North America, their ranges approximating that of the tropical and subtropical parts of the New World at the present time.

Following the extinction of certain snake genera in the Miocene, the Pliocene marks, with few exceptions, the first occurrence of Recent genera found in North America. This period thus represents a time in which snake faunas were becoming modern in their general aspect. Zoogeographical distribution of snakes on the generic level was probably similar to that of the present time. In North America the Viperidae made their appearance in the (?) Lower Pliocene of Driftwood Creek, Nebraska (Brattstrom, 1954a), and are found in the Middle Pliocene of Florida. *Lampropeltis* and *Heterodon* are present in the Pliocene of Central and Western United States and Mexico (Brattstrom, 1955a, 1955b; and Peters, 1953). *Heterodon, Stilosoma, Diadophis,* a crotalid (*Crotalus?*), and an elapid (*Micrurus?*) also occur in the Middle Pliocene of Florida.

However, all the Pliocene snakes reported represent species distinct from the Recent generic representatives (with the exception of *Agkistrodon contortrix*), and apparently are ancestral to at least some of the Recent forms.

Only two extinct North American Pliocene genera have been recognized nomenclatorialy: *Paleoelaphe* Gilmore (which is very close to *Elaphe,* and should be synonymized with it) and *Paleofarancia* (which is *probably* Pliocene in age, and may be ancestral to either *Farancia* or *Abastor*, or both).

On the basis of data obtained from the amphibians of the Florida Middle Pliocene locality of Haile VI (Auffenberg, 1956b) there is every reason to believe that it was between Lower Miocene and Middle Pliocene that Florida felt the effects of a western herpetofaunal immigration. This is also suggested by the presence of certain genera of snakes in the Middle Pliocene which are thought to have their ancestral home in southwestern North America (*Crotalus, Micrurus*, etc.).

There is no evidence that either of the Floridian endemic genera of snakes (*Liodytes, Stilosoma*) evolved in Florida. *Liodytes* is, perhaps, a form that evolved in southeastern United States, but its extreme similarity to *Helicops* makes one wonder whether these two genera simply represent relict populations of a formerly much more extensive stock. The Florida worm lizard, *Rhinura*, is today found exclusively in the Florida peninsula, though as a fossil it is known from several widely scattered Oligocene localities in western, north-central United States. *Stilosoma* is reported from the Pliocene of Florida, a time when it is believed that immigrations from more western parts of North America were being felt in the peninsula. *Rhinura* and *Stilosoma* (as well as *Neoseps?*) probably entered Florida at this time.

Paleofarancia, from the Pliocene of Florida, is here considered as a possible ancestor of *Farancia* and/or *Abastor,* two Recent genera more or less restricted to southeastern United States. However, *Paleofarancia* is provided with vertebrae which, although more similar to *Farancia* and *Abastor* than to any other Recent North American snake, are distinctive. It may represent the culmination of a line which became extinct near the beginning of the Pleistocene, ancestral to no modern forms.

The Pleistocene deposits of Florida present a complex series of beds, deposited locally and of a remarkably uniform faunal composition. Many of these bear indications of admixture with more recent faunas. A large percentage of the fossil forms, mammalian and otherwise, are identical to Recent animals existing in the same area at the present time.

Hay (1923) believed that some of these deposits represented Nebraskan time, but the modern concensus places them in Middle Pleistocene, Late Pleistocene, and Pleistocene and/or Recent. Thus, no Early Pleistocene deposits are recognized in the state at present.

Though remarkably uniform in faunal composition on the whole, certain forms, now found to the north of peninsular Florida are present in some of these deposits. Thus, the bog lemming (*Synaptomys*), now found as far south as northern North Carolina, is present in some of the deposits. Similarly, the porcupine (*Erethizon*), the beaver (*Castor*) and the red fox (*Vulpes*) are all found north of Florida at the present time, though they have been reported from various Pleistocene, or Pleistocene and/or Recent localities in the state. Among the birds the ruffed grouse, found as far south as Virginia in historic times, is found in at least one Pleistocene deposit. In the reptiles *Pseudemys scripta* and *Macroclemmys* are found as Pleistocene forms far to the south of their present ranges. *Carphophis amoenus* is found in at least three localities south of where it exists today. *Natrix erythogaster* is also reported from a Pleistocene deposit somewhat south of its present range. The Pleistocene *Pseudobranchus* from Florida, *robustus,* is closest to *striatus,* which at present is restricted to coastal Georgia. *Eumeces fasciatus* is found in a Pleistocene deposit in central Florida, whereas at the present time apparently it is limited in its southward extent to extreme northern Florida.

All of these records suggest Pleistocene glacial climates which were somewhat cooler than those occurring in the area today. Certain forms have been taken as indicative of very cool climates. This is particularly true of some of the mammals. On the other hand, the climatic shift necessary to bring the Georgia-Carolinian herpetofauna into central Florida is not great. Much more important, remains of many of these more northern faunal elements are almost always found with vertebrates generally associated with warmer climates; *Geochelone,* several armadillos, tapirs, capybaras, etc. The presence of the former is particularly important in climatic interpretations. It has not been found to be absent in any of the better known Pleistocene fossil localities of Florida, suggesting that some factor other than temperature may have been responsible for the presumed southward shift of ranges of some more northern types. Greater precipitation during glacial periods may represent one of several such factors. Obviously the problem deserves considerable additional study.

A recent suggestion (Auffenberg, 1958a; Weigel, 1958) was that during the time represented by Stratum 2 at Vero (and deposits at other localities) Florida felt the effects of a migration of certain paludicolous animals. These forms probably migrated eastward along a coastal circumferential Gulf of Mexico route.

At the present time there is at least some evidence to indicate that forms usually taken as indicators of Pleistocene time may have existed until fairly recently in Florida. This has been demonstrated in several other areas in North America. Thus, the mastodon is now thought to have become extinct during, or slightly before Altithermal, or Thermal Maximum time. Winters (personal communication) indicated that the "Pleistocene" forms have not yet been found in definite association with very early indian shell midden material in Florida, other than a few pieces which are presumed to have been collected in a fossil state from some other locality by the inhabitants. Some of the deposits containing extinct vertebrates in Florida are most certainly Post-Pleistocene. Admixture from more recent deposits may or may not be a factor in such occurrences.

Only through further study of the problem of correlation and dating of these deposits can we hope to realize the value of the excellent Quaternary deposits in Florida. It is much too early to speculate intelligently on the age of most of the Pleistocene fossiliferous deposits in the state. Future correlations may alter many of our concepts involving the past history of certain groups, including the snakes.

The most striking fact concerning the Late Pleistocene snake fauna of Florida is its similarity to the modern one. The great degree of extinction witnessed among the mammals and birds in Pleistocene and Post-Pleistocene time apparently is not present in the reptiles. Evidently only one Pleistocene Florida species of snake has become extinct, *Crotalus giganteus*.

As was mentioned above, at least some minor faunal shifting is evident in the Pleistocene mammals of Florida. A similar, though less spectacular change is apparent in the reptiles and amphibians. The exact nature, correlation, and dating of these climatic and faunistic shifts remains uncertain. Brodkorb (1957) suggested that the deposits at Reddick and several other localities represent Illinoian time. A more extensive, but tentative correlation of several Pleistocene localities recently was attempted (Auffenberg, 1958a).

Many students working with Pleistocene glacial phenomena have been struck with the unusual fact that, according to present concepts, each succeeding interglacial period produced marine terrace levels successively lower than the previous interglacial period. Various reasons have been suggested for this, none of them really satisfactory. The simplest hypothesis would call for increasing cooler interglacial periods. Thus the present conditions would be cooler than any of the interglacial periods. Furthermore, in examining the history of Pleistocene marine terrace study one is impressed with the feeling that we are choosing our terraces to fit the known glacial and interglacial history. At least in Florida many of the terraces are difficult to distinguish, and marine fossils are missing in many of them. Conditions similar to those which produced the Miocene shell-bearing clays and marls certainly should have been present in Florida. If so, the contained fossils would not have been leached out, since they had not done so in the much earlier deposits.

Much of the correlation of the Pleistocene fossil deposits of Florida will rest on the final determination of the mode and time of development of the terraces found above, or immediately below, most of these localities. Quinn (1957) recently published a study of the coastal terraces of Texas in which he ascribes these land forms to alternating climates during the Pleistocene, rather than marine erosion and deposition. Whether or not he is completely, or even partly correct is unknown at present, but it is stimulating to see a new approach to the problem of terrace levels in the circumferential Gulf area.

Most of the mammals which became extinct in Pleistocene or Post-Pleistocene represent large forms. Man has been suggested as being the most important factor in this selective extinction. Also he may have been responsible for the extinction of the only three extinct Pleistocene reptiles in Florida, *Geochelone, Terrapene c. putnami* and *Crotalus giganteus:* all giant forms when compared to modern related genera or species. Primitive North American peoples are known to have eaten box turtles and rattlesnakes. There is little doubt but that even more ancient inhabitants of Florida also ate them. However, it is difficult to see how men could bring about extinction of animals such as box turtles and rattlesnakes, regardless of size. The giant land turtles are, however, a different proposition. Large turtles related to the genus *Geochelone* are eaten the world over by people of all races. Man has, in fact, brought about the extinction of several species of this turtle during historic times. Pieces of *Geochelone* shell have been found in at least one shell midden, although it is not certain whether or not the remains pertain to an animal alive at that time. Presumably the fragments were picked up elsewhere and carried to the midden as a curio (Bullen, 1956). It is much more likely that the extinction of all of these Pleistocene reptiles was brought about by some changing climatic factor. If the Pleistocene was indeed a period of fluctuating, but increasingly colder stages possibly the cold tolerance of these reptiles was surpassed only during the Wisconsin, and they lived in Florida continuously throughout the earlier part of the Pleistocene. On the basis of present and Pleistocene distributions of some of the reptiles and amphibians in Florida, apparently there is a group composed of a number of genera and species which at present are found only in northern Florida, but which during the Pleistocene extended much farther southward. Among the snakes this includes only *Carphophis* and *Natrix erythrogaster*. By inference, through coincidence of distributional patterns, *Crotalus horridus, Natrix rigida, Natrix septemvittata, Storeria occipitomaculata* (?). *Haldea striatula*, and *Agkistrodon contortrix* should be included in this group. All of these are more northern forms, apparently reaching their southern extent in northern Florida. They may be re-entering Florida since their maximum northward extension in Thermal Maximum, or Altithermal time. Finer techniques of collecting and identification of fossil snake vertebrae probably would show at least some of them present in the Pleistocene of central Florida, as in the case of the distinctive species, *Carphophis amoenus* and *Natrix erythrogaster*.

From the standpoint of vertebrate fossils, the most important contributions yet to be made to our known history of the faunal changes of the Post Pliocene in Florida are concerned with the Early Pleistocene and Post Pleistocene. The latter seems unimportant as regards the fossil reptiles of Florida (disregarding the extinction of a few forms). The early Pleistocene of Florida, however, would be extremely interesting from a paleoherpetological viewpoint, as apparently before this period most of the modern species became established. It is hoped that further prospecting or some reliable method of dating applicable to these deposits will disclose localities representing this period.

VII. SUMMARY

Fossil snakes are now known from three geological epochs in Florida: Miocene, Pliocene, and Pleistocene.

Miocene snakes have been found at only one locality in Florida: Thomas Farm, Gilchrist County. The snake fauna from this deposit includes aniliid, boid and colubrid genera. This is the first record of fossil Aniliidae from eastern North America. A new genus and species is described: *Anilioides minuatus*. The Miocene colubrid genera represent the earliest occurrence of this family in the New World. Two new genera and species are described. *Pseudocemophora antiqua* and *Paraoxybelis floridanus*. The former possibly is related to the modern genera *Cemophora* and/or *Lampropeltis;* the latter seems to be close to the Central American *Oxybelis*. The family Boidae is represented by *Pseudoepicrates* (gen. nov.) *stanolseni, Ogmophis pauperrimus,* and *Calamagras floridanus* (sp. nov.). The genus *Neurodromicus* Cope is considered a synonym of the crotalid genus *Sistrurus;* the fossil boid *Neurodromicus barbouri* Vanzolini a synonym of *Pseudoepicrates stanolseni* (Vanzolini).

Pliocene fossil snakes are known from only two localities in Florida, Haile VI A, Alachua County, and Lithia Springs, Hillsborough County. They are all referred to the family Colubridae. One new genus and species, *Paleofarancia brevispinosus,* may be ancestral to *Farancia* and/or *Abastor*. Three additional new species are described: *Heterodon brevis, Diadophis elinorae,* and *Stilosoma vestustum*. Specifically unidentifiable crotalid and elapid vertebrae are known also from this epoch in Florida.

Pleistocene snakes are now known from about 23 localities in Florida. The species identified from these deposits include the following colubrids: *Carphophis amoenus, Farancia abacura* (and/or *Abastor erythrogrammus*), *Diadophis punctatus, Rhadinea flavilata, Heterodon simus, Heterodon platyrhinos, Opheodrys aestivus, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Elaphe guttata, Elaphe obsoleta, Pituophis melanoleucus, Lampropeltis doliata, Lampropeltis getulus, Tantilla coronata, Storeria dekayi, Natrix sipedon, Natrix cyclopion, Natrix erythrogaster, Natrix taxispilota, Liodytes alleni,* and *Thamnophis sirtalis.* The family Elapidae is represented by *Micrurus fulvius*. Crotalid snakes include *Agkistrodon piscivorus, Sistrurus miliarius, Crotalus adamanteus,* and *Crotalus giganteus.*

The fossil species *Crotalus pleistofloridensis* Brattstrom is referred to the synonymy of *Crotalus adamanteus. Crotalus horridus* may be present in several deposits, but the fragmentary and isolated vertebrae available cannot be separated with certainty from *C. adamanteus. Crotalus giganteus* represents the only Pleistocene species of snake in Florida known to be extinct.

The fossil snake material from Florida suggests some faunistic shifting in the peninsula during the Pleistocene. These are assumed to be correlated with shifting climatic zones during the same period. Two species of snakes, *Carphophis amoenus* and *Natrix* *erythrogaster,* are known from fossil localities in Florida which are located south of their present ranges.

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